BODY REPRESENTATION AND MOTOR IMAGERY: EFFECTS OF ADAPTABILITY

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Summary

We are occupants of a body that receives diverse sensory input via our visual and somatosensory system. Furthermore, as we are the agent of our own body, the brain must also deal with both the afferent and efferent signals that occur with movement, namely the motor system. How do we perceive our stationary or moving body as well as the world around us as a coherent whole? Mental representations are assumed to support and modify our perception, as well as the resulting behaviour, the action. In this thesis, representational processes in the perception of the body and its movements are discussed in relation to the particular systems: *vision, somatosensory, and motor*.

In chapter 1, the *general introduction*, the terms 'representation' and 'images', as well as 'body representation' and 'movement representation' are described along the lines of previous research and defined for their appropriate use within this thesis. Specific background literature and concepts with respect to the experiments are discussed in the introductory sections within each individual chapter. Chapters 2 and 3 explore representations of the stationary body by the sensory modalities vision, proprioception, and touch, whilst chapter 4 deals with mental representation in movement. Overall, the results of these investigations exemplify the adaptability of representational processes based on different sensory systems in the stationary and the moving body (see chapter 5).

The three experiments combined in chapter 2 investigated *body representations based on the visual sensory system*. The question was, to what extent does the form of what we visually perceive influence our mental transformation processes? All three experiments gave evidence that different

forms of body representations in response to vision are behaviourally not as disparate as suggested by previous investigations. For example, participants needed more time to mentally transform visually presented stimuli with increasing angular disparity between them. This was the case for abstract objects as well as for bodies when no rotation in depth was necessary (Experiment 1). The response pattern for identifying the outstretched arm in a body figure was thus comparable to that when identifying abstract objects. Hence without depth rotation, egocentric body transformation is akin to mental object rotation. In contrast to the hypothesis on effects of expertise, however, no effect could be observed between subjects: The reaction times between dancers, who are experienced in mentally transforming bodies, and novices did not differ significantly (Experiment 2). Surprisingly, when body postures were presented in the abstract dance notation of Laban (Experiment 3), no mental rotation costs were measured. These three experiments showed that mental transformations were available in different prospects, of which one is perspective-independent. Consequently, in certain conditions the mental presentations seem to switch quickly from a perspective dependent to an independent form. Accordingly, mental representations are not singularly dependent on the presentation form. Cognitive processing of either visually perceived abstract objects, body drawings, or body-related symbols were comparable, whereas the spatial frame of reference, the orientation between the observer and the perceived orientation of the stimuli, was of primary relevance. The type of visual presentation only defines the form of mental representation used for the transformation when a mental rotation in depth is needed.

The experiments in chapter 3 looked at how we sense the *body in egocentric space based on somatosensory perception*. In particular, the first of these psychophysical investigations was concerned with the perception of body limbs in space, that is, proprioceptive sensory mode (Experiment 4). The second was an experiment on tactile perception on the body surface, that is, tactile sensory mode (Experiment 5). Proprioception is the sense which is thought to give us the experience of our own body posture. The tactile sensory mode consists of two distinct perceptual processes: the tactile experience itself (tactile recognition) and the localisation on our body surface (tactile localisation). Both proprioception and tactile localisation revealed effects of adaptability on body reference points. The experiment on proprioception showed that actively pointing to a location in egocentric space is biased by two reference centres of the body located at each shoulder in all but the visual condition. Dancers showed a smaller bias of the two reference centres; but interestingly, they also showed it in the visual task. Therefore, the perception of the self in egocentric space referred to different functional body references according to both the sensory modality used and the individual's motor expertise. Moreover, the modality can be substituted with simulation, such as simulated proprioception in the dancers' group. The experiment on tactile localisation showed that the point of sensations of touch was located closer to the body centre than the original stimulation. This was the case in both sensory modes that were available to localise a point of touch: vision (by visual estimation) and motor (by pointing). Thus, the body centre acts as a reference point independent of the response mode. Interestingly, additional tactile information from the tip of the finger caused a switch in the direction of the mislocalisation from the body centre to the periphery. Consequently,

representations of the egocentric space are adaptable in both the short- and long-term, and this adaptability is dependent on both sensory input and expertise, respectively. Further, tactile perception is immediately integrated in the perception of the body space and has a dramatic effect on spatial localisation on the body surface.

Chapter 4 discusses *how movement representations can evolve by motor imagery training* compared to common execution training. Mentally rehearsing the abduction of the big toe, a movement without established motor command, caused a reduction in the time taken to move whereas exertion force was most increased by execution training (Experiment 6). This finding shows conceptually different training effects between imagery and execution. It goes beyond previous behavioural studies that have shown differences between imagery training and execution training in the level of performance increase alone. In addition, a representation of the movement goal (anticipation) surprisingly improved participants' movement abilities, as could be observed by a performance increase in the movement range of the abduction. Thus along with representations of the stationary body, mental representations can be consciously instrumentalised in the moving body, such as motor imagery or anticipation; they can also show short- and long-term performance adaptations, respectively.

Chapter 5 is a *general discussion* of the experimental results. The data from this thesis supports the existence of a nonmodular adaptable body representation that can accommodate long-term changes (through experience) as well as rapid switches (from different sensory feedback information). Representations are hypothesised to be the effect of adaptability processes. In addition, the importance of differential observation is highlighted.

Zusammenfassung (Summary in German)

Der Körper ist unser Instrument, mit dem wir uns in der Welt zurechtfinden. Űber die verschiedenen Sinnessysteme des Körpers können wir unsere Umwelt sowie die ‚Körperinnenwelt' erfahren. Das visuelle System ermöglicht ein Abbild der Aussenwelt. Das somatosensorische System, bestehend aus der Propriozeption und der Berührungsempfindung ist wichtig, um die Position unseres Körpers im Raum sowie die Gestalt unseres Körpers wahrzunehmen. Nebst diesen im passiven Körper vorhandenen Sinneseindrücken haben wir aber auch Bewegungsempfindung: Wir sind nicht nur Empfänger von Sinneseindrücken, wir agieren aktiv mit unserem Körper in der Umwelt. Im Gehirn findet ein Zusammenspiel sowohl von solchen afferenten als auch efferenten Signalen statt. Wie aber ist es möglich, dass wir trotz der Information von verschiedenen Sinnessystemen unseren passiv oder aktiv (bewegten) Körper sowie die Welt um uns herum als eine zusammenhängende kohärente Entität wahrnehmen? Mentale Repräsentationen sind ein zentrales Element in diesem Integrationsprozess: Sie spielen eine wichtige Rolle in dem Zusammenspiel von Wahrnehmung und resultierendem Verhalten (die Handlung). In dieser Arbeit werden mentale Repräsentationen der Wahrnehmung des Körpers und seiner Bewegungen in Bezug auf die besonderen Sinnessysteme besprochen: visuelle, somatosensorische und motorische Sinneswahrnehmung.

Das erste Kapitel gibt eine *Einführung in die Begriffe* Repräsentation und mentale Bilder, sowie Körperrepräsentation und Bewegungsrepräsentationen. Insbesondere wird der spezifische Gebrauch der Begriffe innerhalb dieser Arbeit

definiert. Weitergehende Einführungen sind in den Einleitungen der jeweiligen experimentellen Kapitel zwei bis vier zu finden.

Die *mentale Körpertransformation basierend auf dem visuellen System* wird in Kapitel zwei besprochen. In Experiment 1 wurden die Prozesse in der mentalen Rotation von Objekten und Körpern untersucht. Dabeit hat sich gezeigt, dass insbesondere die Rotation in der Tiefe das Verhalten der Versuchspersonen beeinflusst. Versuchspersonen benötigen für die Diskriminierung zweier abstrakter Objekte in der Regel länger, je grösser die Diskrepanz in der Ausrichtung der zu beurteilenden Objekte ist. Dieser Rotationseffekt konnte auch bei der Identifizierung von Körperstimuli nachgewiesen werden, jedoch nur wenn die Ausrichtung der Stimuli mit der egozentrischen Perspektive der Versuchsperson übereinstimmte, das heisst, wenn keine Rotation in der Tiefe notwendig war. In Experiment 2 wurde der Einfluss der generellen Bewegungsexpertise von Tänzern auf die mentale Transformation von Körpern untersucht. Die Daten der beiden bis auf die Probandengruppe identischen Experimente 1 und 2 zeigten keinen Unterschied zwischen Tänzern und nicht-Tänzern in Bezug auf die mentale Körperrotation. In Experiment 3 wurde schliesslich untersucht, welchen Einfluss die Form des visuell präsentierten Körpers auf die mentale Repräsentation und Transformation hat. Dazu wurde in der Hälfte der Bedingungen der Körper in der Labanotation, einer etablierten Tanzschrift dargestellt. In der Labanotation werden arbiträre Symbole für die Darstellung der verschiedenen Körperglieder verwendet. In der Diskriminierung zweier Körperpositionen in unterschiedlicher Orientierung haben sich erhöhte Reaktionszeiten nur bei Stimuli in Form von Fotos einer Tänzerin, nicht aber in Form von abstrakter Labanotation gezeigt. Das heisst, die mentale

Repräsentation von Körpern und/oder deren Prozesse sind perspektiven-unabhängig, wenn die Repräsentation von arbiträren visuellen Körperstimuli generiert wurden. Die drei Experimente im ersten Kapitel zeigten, dass die Repräsentation von Körpern und Objekten sowie deren mentalen Transformation von der Form der visuellen Stimuli und insbesondere auch von deren Orientierung abhängig ist. Die Prozesse der Repräsentationen zeigten sich teilweise bei identischer primärer visueller Darstellung unabhängig und teilweise abhängig von Perspektivenwechsel. Dieser Effekt lässt eine hohe Adaptabilität der Repräsentation von Körpern basierend auf visueller Wahrnehmung vermuten.

In Kapitel drei wird die *Verarbeitung und Wahrnehmung des Körpers im egozentrischen Raum basierend auf somatosensorischer Empfindung* untersucht und dargestellt. Im vorhergehenden Kapitel hat sich gezeigt, dass die Perspektivenabhängigkeit, und somit der egozentrische Referenzpunkt der Körperrepräsentation von den visuellen Stimuli beeinflusst ist. Die Experimente 4 und 5 untersuchten die Referenzpunkte innerhalb der Wahrnehmung des eigenen Körpers in der motorischen Interaktion im egozentrischen Raum. Mittels Experiment 4 konnte gezeigt werden, dass die beiden Schultern als Referenzpunkte wirken, wenn Probanden Punkte im Raum lokalisieren mussten. Die Bewegungserfahrung von Tänzern jedoch führte erstens zu geringeren Schätzungsfehlern basierend auf einem Referenzpunkt im Körperzentrum. Zweitens zeigten Tänzer dieselben Abweichungen in der Lokalisierung bei visuellem wie bei propriozeptivem Feedback. Möglicherweise haben die Tänzer in der visuellen Bedingung ein ‚virtuelles' propriozeptives Feedback generiert. In Experiment 5 mussten die Probanden taktile Berührungspunkte auf dem Arm lokalisieren. Die Punkte wurden konsistent zu nah am Körper geschätzt. Wenn

die Probanden jedoch zusätzlich taktile Stimulation am Finger erhielten, kehrte sich die Unterschätzung der Distanz vom Körperzentrum zum Berührungspunkt in eine Überschätzung um. Eine kurzfristige Integration zusätzlicher Berührungspunkte wurde vermuted. Beide Experimente zeigten unterschiedliche anpassungsfähige Körperreferenzpunkte, kurzfristig in bezug auf die vorhandene sensorische Information sowie langfristig basierend auf Erfahrung.

Schliesslich wird in Kapitel vier der Einfluss der *motorischen Vorstellung auf die Bewegungsrepräsentation* untersucht. Es hat sich gezeigt, dass mentales Training und physisches Bewegungstraining sich nicht nur in der Intensität unterscheiden, sondern vermutlich zwei verschiedene Prozesse sind. Mentales Training führte zu einer rascheren Ausführung der erlernten Bewegung während Bewegungstraining die Kraft erhöhte. Die Bewegungsrepräsentation ist daher unterschiedlich adaptiv, abhängig davon, wie sie angesprochen wird.

Die Befunde der Experimente 1 bis 6 werden in Kapitel fünf *diskutiert*. Mentale Repräsentationen zeigten sich in dieser Arbeit über verschiedene Sinnessysteme hinweg anpassungsfähig. Die Resultate lassen vermuten, dass die effiziente Interaktion mit der Umwelt durch einen adaptiven Mechanismus mentaler Repräsentationen ermöglicht wird. Repräsentationen in dem Sinne können als Effekte der Adaptabilität verstanden werden. Unter dieser Annahme wird das aktuelle Forschungsvorgehen diskutiert. Jeder Körper, jeder Geist sowie deren assoziierten Repräsentationen haben sich adaptiv an die Umwelt angepasst und tun dies kontinuierlich in einem individuellen Sinne. Um adaptive Prozesse in der Kognition zu entdecken, scheint es entgegen dem gebräuchlichen methodischen Vorgehen angebracht, das Augenmerk auf individuelle Ausprägungen zu richten.

Chapter One

General Introduction

The perception of our human bodies and their movements is a fascinating subject for both scientific research and everyday life. We experience ourselves and a sense of agency of our own body by integrating information from different sensory systems. For instance, while typing this sentence, I can see my hands on the keyboard while I sense the fingers' positions as I feel the touch on my finger tips. Besides the sensation of our own body, the visual perception of other stationary or moving bodies can be a pleasurable experience, an example of which is the form of dance. Dance also illustrates several aspects of body and movement representations. For instance, dancers use various techniques in imagery and training in order to improve their physical performance and emotional expression. For that reason, dancers have often been used as experts in recent scientific research (for a review see Jola & Mast, 2005). In this thesis, dancers were tested as experts in all but one experimental study. However, as well as dancers, any healthy individual has a clear sense of one's own body. Combining the body's movements and its position in space is a generic ability and gives a sense of what it means to be oneself.

The cognitive and neuronal mechanisms underlying self-related perceptions of the body are intriguing and challenging to study scientifically, because representational processes are not directly accessible. For instance, while movement characteristics can be classified by visual observation, the

mental processes in response to particular movement characteristics cannot: When a dancer learns a new movement pattern, he or she can verbally describe the movement characteristics, but these do not necessarily have to correspond with the features of his or her representation of the movement. Neuronal activation from sensory inputs of a stationary body can be inferred from data of current methodological techniques, such as functional magnetic resonance imaging (fMRI). Further, how the body and its movements are experienced and accordingly represented in the mind, is subject to interpretation from data collected by behavioural experiments (e.g., Calvo-Merino, Jola, Glaser, & Haggard, 2008). To clarify, instruments to extract and analyse movement parameters do exist: When watching a dance performance, body orientations, gesture directions, movement speed, and body limb alignments can be perceived and analysed with the help of systems, such as the Bartenieff Fundamentals principles (Hackney, 1998). The changes in movement quality can be detected with such movement analysis systems and be used to compare training effects (e.g., Barnea, 2006). Yet the captivating question of how the performance is represented in the dancers', the choreographers', or the audiences' minds, goes beyond pure visual perception. In order to understand and model mental processes, a scientific approach is required.

The experimental studies presented in the following chapters focus on the body and its movement representations separately. The fact that we are constantly moving has to be integrated in the body representation. The ability to move constitutes our perception of the world. However, it is only recently that the relationship between the body and its movement representations has been investigated. Most studies on bodily representations have focused on the

stationary body, even though they have incorporated aspects of movement. In this thesis, body representations in the stationary body are discussed with respect to different sensory modalities, and movement representations in the moving body are investigated by a motor learning experiment. The representation of the self based on different sensory modalities is discussed in chapter 2 and 3, whereas chapter 4 deals with motor imagery and visualisation effects on movement representations.

It is important to investigate both body and movement representations in order to capture similarities, such as the feature of adaptability. For example, over the centuries, dance styles have changed dramatically and the connotation of the body has undergone immense cultural changes. Thus body representation as well as movement representations are thought to be highly adaptable. On the one hand, characteristics of the body representation can be influenced by movements. On the other hand, movement types seem to be dependent on particular body representations. However, how movements are generated and what role the body representation plays in movement is less clear. Furthermore, the way in which particular movement types modify the body representation itself remains unresolved. This thesis is considered a first step into the novelty perspective of looking at body and movement representations by their adaptability alone. Further studies investigating how the body directly affects movement representation and how movement affects body representation would extend the current investigation and should be considered for future research.

In the following sections of the introduction I will highlight some of the few earlier experimental works that initiated the study and development of mental representations and which reflect properties in mental representations relevant

within this thesis. Furthermore, current concepts of body and movement representations will be outlined to position and structure the content of the present work. Detailed information and references related to each experimental work are outlined in the introductory sections within each particular chapter.

Mental Representations and Mental Imagery

Definitions

In general, a *representation* is a substitution in the absence of the thing it refers to, most often something in the external world or even something mentally generated (Eysenck & Keane, 2000). In cognitive neuroscience, the term 'representation' has many different meanings. Mental visualisations, such as visual images, generally represent objects or actions. Further, representation is used for mere unconscious mental surrogates, often described by the terms 'schemata' and 'template'. However, representation is also used to describe the somatotopical organisation of the body in the somatosensory and motor cortex. The term 'representation' is also closely related to 'mental images', yet the distinction is not always clear (Cooper, 1995). Several forms of mental images have been reported in the literature on imagery research over the past 20 years. In particular: *visual* images representing real perception in a depictive way (e.g., Kosslyn, 1996), *spatial* images representing spatial relations among entities (e.g., Johnson-Laird, 1983), and *motor* images representing the motor action from an egocentric perspective (e.g., Annett, 1996). Not only the content but also the processes related with these images are proposed to be different. Operations

such as mental rotation and mental scanning of visual images are seen as isomorphic to corresponding operations on real perceptions, whereas the construction and manipulation of spatially organised mental models only represents a possible state of affairs described in the premises independent of visual processing (Knauff, Jola, & Strube, 2001; Knauff, Strube, Jola, Rauh, & Schlieder, 2004). Further, motor imagery is viewed distinctive from visual imagery in respect to its inherent egocentric perspective (Jeannerod, 1995) as well as its neural substrate (Decety & Jeannerod, 1995). Jeannerod implies that in motor imagery, "the subject feels himself executing a given action, whether it involves the whole body (e.g., running), or it is limited to a body part (e.g., writing, pointing to a target or holding pressure against an obstacle)" (p. 1420).

In this thesis I consider 'representation' as the internal conceptualisations derived from multiple sensory information of either side of the body; the world around us and the inside. I use the term 'mental images' with respect to Jeannerods' (1995) view on motor imagery. His idea is that motor imagery is part of the motor representation which is unconscious but can be accessed consciously under certain conditions: A motor image is a conscious motor representation. Thus, an 'image' delineates the conscious accessible part of a 'representation' which can be experienced either as *pictorial* or *kinesthetic*. However, both mental representations and mental images are based on multisensory information and they both inherently contain phenomenal experiences which are partly voluntarily perceivable and partly controllable (see p. 25). Besides bottom-up information from sensory receptors, mental representations and images can also be generated and modulated top-down by cognitive processes, such as mental simulation. It is probably the multisensory

aspect that has led to several distinct definitions. For example, as mentioned above, mental images are often subdivided into motor images, visual images, and kinesthetic images. Correspondingly, mental representations were mostly investigated as either visual or motor representations. To summarise, representations and images are not used interchangeably within this thesis. The term 'representation' is defined as a superordinate concept for cognitive processes that provide perception of the body, its movements, and the world around us. Mental *images*, however, are used to describe forms of representation that are consciously experienced.

History

The foundation of the current research on mental representation is built on three classic experiments. The tradition of research on mental representation processes started with the work of Tolman (1948). He showed that mice who were food deprived found the shortest yet unknown way to the food when the previously learned path has been restricted. Tolman concluded that this was only possible because the mice constructed a cognitive map of their environment. He was the first of the Behaviourists who made clear suggestions on cognitive processes instead of looking at the brain as a *black box* situated between stimulus and behaviour. Today, years after Tolman's finding, cognitive maps and other forms of mental representations are widely accepted to play an important role in human cognition.

The next important step that has been taken in research was by Shepard and Metzler (1971). The authors' experimental work shed light into the transformational processes of mental representations. In their classical mental

rotation task, participants were presented with two abstract cubes in different angular orientations while they had to identify whether the stimuli were identical or not. The experiment revealed that participants took longer to respond when the orientation disparity between the two cubes increased. This increase in reaction time with increasing angular disparity has since been regarded as the expression of the rotation time needed to align the two objects mentally, according to real rotation time. For the first time, strong evidence for functional processing of mental images was revealed.

Finally, new brain imaging techniques such as functional magnetic resonance imaging (fMRI) enabled further insight into the neuroanatomical correlates of mental representations and mental transformations. Kosslyn et al. (1999), for example, was one of the first to show brain activation correlates in visual areas during visual imagery. This finding supported the existence of visual imagery as well as its modular characteristics.

These three basic steps differ firstly in their propositions on the spatial content within the representations and secondly with regards to their propositions about neuronal manifestation. Ever since, these features remain as the basic differences between scientific investigations on mental representations. First, mental maps (i.e., Kosslyn, Ball, & Reiser, 1978; Tolman, 1948) are supposedly mental representations of spatial maps inherently containing spatial relations. Mental representations (i.e., Shepard & Metzler, 1971) have a spatial content, but the spatial relation is referenced between the objects, while the spatial reference frame of the observer, the participant, remains fixed. The spatial relations in mental maps can be perceived either from an egocentric or allocentric perspective. From an egocentric viewpoint, the observer can flexibly modify his or

her frame of reference. This means, a perspective change of the observer can be achieved by egocentric mental transformation. However, in the allocentric perspective, the map is an external representation, which is adjusted according to the spatial orientation of the observer. It was only a decade after mental object rotation was defined by Shepard and Metzler that the egocentric reference frame was taken into account (Parsons, 1987a, 1987b). In these tasks, bodies or body parts instead of objects had to be identified by the participants. In this thesis, differences between mental rotation of objects, bodies, and symbols are investigated in chapter 2. Second, unless otherwise stated, concepts of body and movement representations are investigated herein regardless of their neuronal manifestation. This study investigates behavioural effects of representations rather than neuronal substrates of representations. Nevertheless, the 'hardware' of representational processes may indeed play any role in how cognitive processes are actually implemented in the brain and how neuronal manifestation restrict or enable cognitive processes. For a general understanding of the human brain, the neuronal substrate of representations must be taken into account. Nevertheless, this can be done in addressing functional properties of representation processes on different levels. Marr's (1982) three independent level discrimination in cognitive modelling – computational, representation, implementation – is addressed (see p. 21) in order to understand the level of investigation within this thesis.

Functions

Do we really need mental representations? What is their functional role? Mental representations are thought to play a role in visual recognition and object

identification (Kosslyn, 1996). For example, when we look at a photograph of a former friend, we are able to recognise our friend when the representation stored in our memory matches the representation of the photograph we are actually looking at. Consider that we are not very sure about whether the person is really the one we have in mind. We can verify this by identifying particular known facial or bodily features as well as behavioural characteristics of our friend. For example, if he or she is writing a letter in the photograph, we can identify the writing hand. To do so, we can easily think ourselves into the person in the photograph and feel which hand is holding the pen. This means we are able to transform the mental representation of ourselves into the visual representation of the body in the photograph. In accordance with Kosslyn's model, recognition is dependent on visual representations whereas identification relies on associative memory and includes multimodal inferences. As in the example outlined above, to identify whether it is the left or right arm with which we 'feel' the pen, we need to have a sensation of our own body. This internal body perception or proprioception is often called the 'sixth sense' since Sherrington (1906). A clear representation of our body in space is built by using the sensory information from our joints, muscle spindles, and tendons. However, without available sensory information, conceptual knowledge may be used to solve such tasks, as discussed by the role of learned conceptual representations in Experiment 3. Furthermore, in the example outlined above, a change in perspective took place when thinking oneself into the body of somebody else. It is widely debated whether visual representations are viewpoint-dependent or not. When the body is involved in the representation, the viewpoint should be considered as playing an important role (see chapter 2). However, investigations involving tactile or

proprioceptive (body) representations often question the centre of reference within the egocentric perspective (see chapter 2). Furthermore, mental images or representations are sometimes regarded as an epiphenomenon of cognitive processes and their pictorial aspects doubted (Pylyshyn, 2003). The propositional theory, for example, suggests that cognitive processes are not based on the mental images but on computational steps. Conversely, a theory from computational science does not support the idea that observed behaviour is represented as such (Brooks, 1986). The behaviour is defined by the way in which the body is constructed and interacting with its environment. Actions, intentions, and motivations are embodied. What we perceive as motives is interpreted when we observe other species or robotics behaviour – and perhaps even ourselves.

Two points speak in favour of representations. Firstly, our conscious experiences of representations, so-called 'images', and secondly, experimental investigations such as the aforementioned classical studies which showed strong evidence for a functional value of representations. For example, several investigations showed that training by mental imagery demonstrates effects on motor performance (see chapter 4). Even if some images were just by-products, experimental investigations have revealed evidence that at least some forms of images are substantial parts of cognitive processes. However, part of the mental representations – unlike mental images – cannot be accessed at all (see sections on body and movement representations below). It is not entirely clear whether mental representations do exist, whether they are implemented in the cognitive processes, or whether these representations are just concepts that evolve when we try to infer models of the brain's functions by experimental approaches. Even

though the representations outlined herein are just explanatory, they further the understanding of functional processes in the cognitive apparatus. Consequently, it is important to clarify the level on which mental representations are investigated.

Marr (1982) suggested a model with three levels of mental representations: the computational, the representational, and the implementational level. In this thesis, I sometimes refer to questions or experimental evidence on how mental representations are computed or implemented in the neuronal system. However, these are just stated in order to support the findings of mental representational properties. Another regularly stated distinction in different representations is between iconic, abstract, and symbolic form in Psychology as well as between projectional (isomorph) and computational maps in Neurobiology (Paillard, 1991). Representations do not necessarily have to be isomorphic relations of the observed actions or the sensory inputs. I do not claim that representations and the neuronal implementations - or representations and sensory inputs - have to be isomorphically matched. For example, when we observe others' actions or emergent behaviour, we intend to see motivations which we expect to be implemented as such but may not be so. The fact that we immediately apply intentions to perceived actions is further evidence for representational concepts. We build and rely on representations within the whole process from recognition to understanding to action. Therefore, it might even be possible that we do not process the images or representations themselves, but represent particular features. The understanding of how these features are processed can be well explained by models of mental representations.

To sum up, the idea is that models of representation help explain a concept or process within cognitive functions. I do not claim how representations are materialised in the cognitive processes, but rather focus on how mental representations are organised.

Sensory Systems

Since cognitive maps were introduced by Tolman (1948), experimental investigations on mental representations have increased enormously and have led to a number of supposedly distinctive forms. Some examples include: (a) maps in spatial cognition such as egocentric maps and allocentric maps, (b) body representations such as body image and body schema as well as (c) visual or motor images, which are widely discussed and described in more detail below. The investigations have often been separated with respect to the sensory mode of perception (vision, touch, proprioception) instead of common features in transformational processes. Correspondingly, this thesis is structured by the sensory systems that led to the representation.

In the literature, sensory systems are classified either by sensory organs (eyes, skin, nose, etc.) or by neurophysiological pathways (visual, tactile, proprioceptive). Each sensory system is thought to be cortically represented in different anatomic areas. For instance, in the visual sensory system, the external world is perceived by projection of visual features from the sensory organ, the eyes, to the occipital areas of the brain. Further, the somatosensory system enables identification of objects in the external world through both touch and the proprioceptive (or kinesthetic) sense, together also referred to as the haptic sense (Gibson, 1962). Information about the position of body limbs in space and

the detection of tactile stimulation on the body surface is projected to the somatosensory cortex from muscles, tendons, and joint receptors in the former and skin receptors in the latter. The proprioceptive sensory mode is also responsible for detecting internal sensory states such as temperature and pressure which are represented in different areas of the human brain. Even though this thesis is structured according to this cortical modularity of the sensory system, the concept of mental representations and images used is distinct from cortical representation. The functional role of a mental representation or image can be distinguished from cortical representation as supported by experimental evidence and subjective experience. For example, the size of the receptive field of a particular body area is corresponding to its size in the somatosensory and motor cortex. Thus, the area of a body part in the cortical representation corresponds with the sensitivity of its real surface. Furthermore, the spatial organisation of body parts in the cortex does not match with that of the real body. Mental representations and images are thus viewed as higher-order representations enabling a coherent perception of ourselves and the world that deals with the body and its neurophysiologic manifestation.

Several psychophysiological and neuronal experiments have shown evidence for different behavioural patterns and neural activations with respect to the particular representation form. For example, several studies disentangled ego- and allocentric neuronal representation (Neggers, Van der Lubbe, Ramsey, & Postma, 2006). Nevertheless, chapter 2 considers different processes within egocentric frames. It will be questioned whether there is a functional argument to define numerous different maps with respect to the different sensory modalities (vision, touch, proprioception, and motor). If the representations based on

different sensory modes share similar features, a superordinate representation may be more applicable than multiple single representations.

Body Representations

The body plays a special role in our existence. We are all occupants of a single body with which we have grown up with over several years. Moreover, we are allied to other bodies for communication purposes. Having a body means having to deal with input from the external world via our perceptual, tactile, and proprioceptive senses. In addition, it also means coping with input from internal states. Nevertheless, the classifications of the sensory systems are manifold. Often, sensory systems are distinguished in relation to the sense organ that constitutes the sense, such as the eye for vision or the nose for olfactory sensation. However, this clear distinction does not hold for the more complex senses of touch and proprioception. The skin might be considered as the sensory organ for touch, but there are also tactile sensations within the body. Also, no single sensory organ is responsible for the sense of proprioception. Furthermore, even within one sensory mode multiple sensory perceptions are possible, such as pressure, temperature, and weight in the tactile mode. In addition, a sensory property can be perceived by different sensory modes as it is the case for spatial relations. The way in which different sensory perceptions from different sensory modes are fused to a coherent experience of our whole body and the world around us remains an intriguing question.

Vision, touch, and proprioception are most important in the perception of our body. For example, when we are touched we can immediately point to the

location on the body where the tactile sensation was experienced. A representation of the body is necessary in order to accomplish such localisation. Sherrington (1906) was the first to define proprioception. Since his early work the position sense, also called ‘sixth sense’ is commonly termed proprioception and thought to give rise to a sense of ourselves. However, the body plays a particular role also in the visual sense. It could be shown that when seeing other bodies relational body information is processed mandatorily (Reed & Farah, 1995).

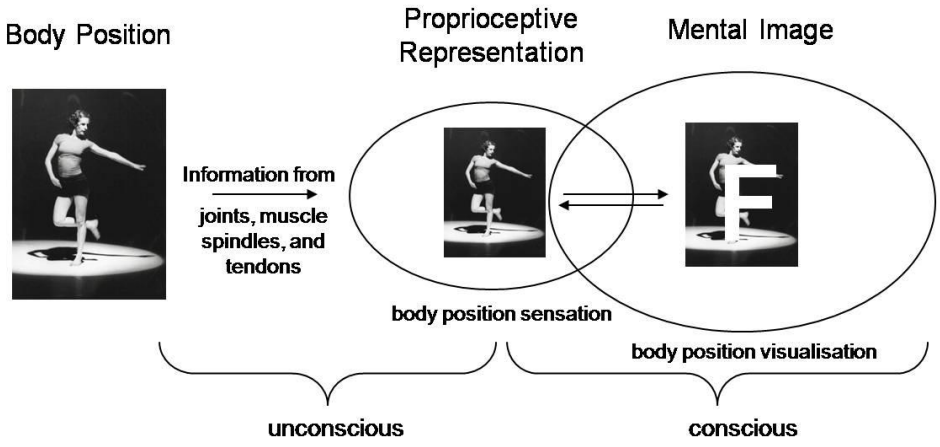


Figure 1: Example of a dance practice. The dancer was instructed to make the shape of the letter ‘F’ with her body limbs. Position information from joints, muscle spindles, and tendons give rise to a proprioceptive representation of the body position while also a visualisation of the letter ‘F’ in form of a mental image can be superimposed on the body position sense.

This thesis investigates body representation in the aforementioned sensory modes, vision (chapter 2), proprioception, and touch (both in chapter 3). These sensory modalities, vision, touch, and proprioception, are not the only modalities relevant to mental representations. Studies that have investigated other sensory

modes, for example audition, have also found evidences for mental representations (De Volder et al., 2001; Haueisen & Knosche, 2001).

Characteristics

The terms ‘body image’ and ‘body schema’ have recently become very popular. Attempts to distinguish between these two representation forms by their functional and neuronal properties are ongoing. Most often, body image and body schema are distinguished by the level of consciousness and their adaptive aspects. The body image is thought to be conscious and closely related to visual perception while the body schema is thought to be unconscious and associated with the motor mode. The body schema is suggested to be especially adaptive with experience. Short- and long-term adaptabilities are necessary as the relation of body parts and the size of our body changes over time whilst we must still be able to make appropriate movements and maintain balance. Despite the suggested distinctions, these two body representations, body image and body schema, are widely debated. For example, Head and Holmes (1911) were the first who mentioned schema in their observations on sensory disturbances from cerebral lesions. In the authors’ view, it is the schema and not the visual or motor image to which body positions are referred to in the instantaneous way:

> When we sit immobile and imagine our fingers touching some object on the table, many of us see, at once, the picture of an outstretched arm; the only image in consciousness is a visual one… the final product of the tests for the appreciation of posture or passive movement rises into consciousness as a measured postural change. For this combined standard, against which all subsequent changes of posture are measured before they enter consciousness, we propose the word “schema”. By means of perpetual alterations in position we are always building up a postural model of ourselves which constantly changes. Every new posture or movement is recorded on this plastic schema, and the activity

> of the cortex brings every fresh group of sensations evoked by altered posture into relation with it. (p. 187).

Therefore, it is worth considering other general characteristics of the representation of the body as discussed below, independently of body image and body schema classifications.

The Body's Reference Systems

The representation of the body immediately questions the reference to the representative's position. It is thought that we are able to position our body within the surrounding environment in different frames of reference. We can either represent our body in an egocentric space or in allocentric reference system. Considering the egocentric space of the individual in question alone, several reference systems are possible within their body. Experimental investigations revealed different reference points within the body, such as the trunk (Mouchnino, Aurenty, Massion, & Pedotti, 1993), the shoulders (Haggard, Newman, Blundell, & Andrew, 2000), or the joints (Cholewiak & Collins, 2003). References such as joints divide the body into different parts. Interestingly, body segmentation is viewed differently for the sensing and acting body (de Vignemont, Tsakiris, & Haggard, 2005) and also with respect to characteristics in neural implementation in the somatosensory and motor cortex. It is therefore necessary to investigate not only body representation based on different sensory modalities, but also movement representation altogether.

The Awareness of the Body's Representation

The aforementioned difference between body image and body schema in consciousness accessibility of the representation is illustrated within the sensory

mode of proprioception in Figure 1 (p. 25). In correspondence with Cooper (1995) a representation can be understood as one form of mental image. While the mental image can be consciously accessed and the experienced cognitive transformations of the image are corresponding to the experimental outcomes, representations also have unconscious elements. As illustrated in Figure 1 (p. 25), the dancer can generate a mental image of her body position. The shape of the body limbs are experienced in a visual representation and matched with the form of the letter *F*. However, can the whole body posture also be mentally perceived in another nonvisual modality, such as the rotation angles of the joints? The spatial orientation and relation of body limbs to each other can be sensed. Such an image is however far more difficult, if at all possible, for the whole body to experience (and that's where the aforementioned reference points come into play). Head and Holmes (1911) describe a patient who never failed to localise where he was being touched, whilst he could not tell the position of his hand. The authors refer to another schema or model of the surface of our bodies which can be destroyed by cortical lesion. Conscious mental representations of sensory modes do not contain the sensory information itself. A good example of the sensory mode of touch was described by Gibson (1962), when he writes about the "Rigidity or Plasticity of the Phenomenal Object":

> When pressing a finger on a rigid surface or squeezing an object with the hand, it is difficult to notice the increase of intensity of cutaneous sensation; instead the observer is primarily aware of the substance and its resistance. Likewise, when pressing or squeezing a nonrigid object (a lump of modeling clay, a rubber ball, a handful of cloth) the observer is aware of the yieldingness, elasticity, or softness of the substance, not of the (very different) intensity of the back pressure on the skin. ... Presumably the degree of force exerted is being registered by the joint-and-tendon receptors and the resulting degree of skin-pressure is being registered by the cutaneous and deep-tissue receptors, but the intensities are not experienced as such. Perhaps it is the *relation* between these different intensities that is registered. The proportion of one to the other,

> and the relative temporal buildup of these two, are different for rigid and for nonrigid objects. A possible hypothesis is that proportion and buildup are registered by the receptive system when it is operating in an exploratory fashion. They constitute stimulus-information about the object, whereas the intensities as such do not. (p. 481).

Important in Gibson's illustration is, that we have a clear perception of how soft or hard the tissue of the touched object is, but we do not perceive the changes in pressure quantitatively. This example again points out how important the transfer from sensory information to mental representation is in our everyday life.

Short- and Long-Term Changes

The possible modifications in the body representation in short- and long-term are other important characteristics that need to be taken into account. For example, the aforementioned reference points can change depending on the sensory input. Furthermore, the body can adapt depending on the sensory information. The experience of a phantom limb shows a certain independence of the representation from peripheral sensory input. A phantom limb sensation is a perception of the lost body part after amputation, sometimes related with pain (e.g., Melzack, Israel, Lacroix, & Schultz, 1997). This representation can, however, be changed by sensitivity training at the corresponding limbs end which results in phantom pain reduction (Flor et al., 1998). Therefore, changes in the body representations are possible by training. In this thesis, the representations adaptability forms an important element. Long-term changes are studied by observing expertise (Experiments 2 and 4) and learning effects (Experiment 6). Short-term changes and adaptations are investigated by modification of the presented stimuli (objects vs. bodies vs. symbols in chapter 2), the available

sensory information (visual vs. proprioceptive in chapter 3) and the sensory system used for the response (visual vs. motor in chapter 4).

Multisensory Fusion

We do not phenomenally experience our body in everyday life in a disparate way dependent on the sensory information from the external world or internal representation states. Thus, although information is processed via distinct neural pathways even within a sensory modality (e.g., Goodale & Milner, 1992), sensory modalities are fused in the experience. Cross-modal effects could be shown experimentally and are important for tasks such as balance and posture. It is therefore important to look at the body representation characteristics across the different sensory systems and also in the way that sensory information corresponds and influences each other.

Movement Representations

The use of the term 'representation' in the field of motor control is not as common as it is for the stationary body. Most proposed models on motor representation, such as comparator models (Bernstein, 1967) or the forward model (Wolpert, Ghahramani, & Jordan, 1995), have two aspects in common. First, the models propose that the motor system is hierarchically organised and second, that a match between the desired and current state of the motor system allows motor control. In this thesis, 'movement representation' is used instead of motor representation to emphasise both the cognitive processes and the movement. The neural instantiation is a necessary aspect to understand the relation between

action and cognition. The focus of mental representations - despite its substantial implementation - can give some interpretational freedom which supports the detection of particular representational properties. Jeannerod (1997), for example, hypothesised that the representation of an internal goal and intention is represented instead of a target or the movement itself. However, when considering motor image, the movement itself is consciously represented. For example, in dance, movements are not object-related and internal goals and intentions have to be represented in relation to the movement in one way or the other. Therefore, the term ‘movement representation’ is used to describe a general form of movement schema which is adjusted accordingly to several sensory bottom-up inputs such as vision or proprioception, as well as top-down control from mentally generated information. A movement representation is responsible for movement execution, the performance, and identification processes when observing movement. These aspects of movement representation are discussed in more detail below.

Performing and Observing Movement

A movement is thought to be a compound of motor preparation, efferent commands from the brain to the acting muscle, and afferent feedback from the muscle to the brain. In short, when a movement is executed, efferent commands along the descending pathways activate the corresponding muscles and afferent feedback information is sent back to the cortical centres (for more detailed information see chapter 4; and Berthoz, 2000; or Jeannerod, 1997). Therefore, whenever a movement is executed, independent of its initiation and familiarity, efferent signals and afferent feedback are provided, as well as their estimates

and copies as proposed by the comparator and forward model. The concept that processes such as intending, imagining, observing/imitating, and performing an action share common structural and functional mechanisms, is widely accepted. Nevertheless, the cognitive processes involved in these different forms of movement generations are yet unresolved. For example, when we imitate a movement, we transfer the movement qualities from perception to action. This process seems to happen without awareness of a movement representation. However, when dancers have to laterally transfer a learned movement sequence, they can do so either by focusing on the changed relation between the body and the space or by focusing on a lateral change within the body. In the former way, no attention is directed on the moved body limb. Therefore as in imitation, no movement representation is experienced as such. Similar to Gibson's example in touch perception (see p. 28), were we are not able to quote exact parameters of pressure, but we have a clear phenomenological experience of the pressure quality; we are unaware of the actual level of the muscle contraction. Jeannerod (p. 187) refers to the interesting statement of Bernstein that the execution involves biomechanical constraints which are not necessarily represented centrally. Thus describing overt action does not allow full access to the central processes and the central processes do not necessarily specify the representation of the action. This means that the overt movement is not a reliable source of information for its own representation. For example, when painting the figure *8* with the right arm in space we can easily recognise the number or draw it while having a mental image of it. We do not consciously represent the movement by joint rotations or kinematic parameters such as the level and timing of muscle contraction as such, but, even so, we move the arm easily along a

visualised 8-path in space. Moreover, from the outside, we see the moving body, but we do not perceive the movements with respect to such points in space. Several good examples of intentions' invisibility without loss of perceptual pleasure can be seen in some dance performances, such as Cunningham's «OCEAN», first performed in Brussels in 1994. The choreographer divided the space into different sections and related the movements to these sections. However, even though the dancers consciously represent the movements with respect to points and lines in space, the audience does not consciously perceive the space but the movements of the dancer's bodies. However, the ability to infer movement intentions when visually observing movements is viewed as highly important in the understanding of others.

Recognition

Clearly, we have the ability to visually recognise a moving body quickly and easily from sparse input. Not only the particular movement itself but also the actor's identity or emotion can usually be identified by the perception of only a few point lights (Johansson, 1973). This effect is known as "biological motion". In the biological motion paradigm, participants are presented with movements indicated only by some point lights placed on the actors' body joints while the body limbs are occluded in the presentation proper. Generally, the task is either to recognise the type of movement (e.g., walking, jumping, etc.) or the type of emotion. Recent research has focused on the difference in identifying or discriminating the actors (e.g., recognise oneself, friends or strangers). Humans are surprisingly good in all these slightly modified tasks. Thus, some functional form of movement representation based on visual input supports the identification of movements. It has also been shown that the visual input can be stronger than the motor

command. Nielsen (1963) found that participants adjusted their own movement on the visual perception of the movement of an alien hand while ignoring the motor information from their own movement. Visual perception on the other hand, seems to be influenced by properties of the motor system (Viviani & Stucchi, 1992). Therefore, what role does a movement representation play in motor control? Moreover, is the skill of recognising human movement based either on visual or on movement experience (or both)? How movements are identified or memorised is not clear. Human movement is the only motion that we both produce and perceive. For that reason it is difficult to assign human movement recognition either to our visual or motor lifetime experience. Dancers have a very particular sense of their motor experience. Interestingly, dancers often insist that the movements are represented and stored in the muscles. This assumption is based on the phenomenological experience when performing a well-learnt movement pattern in a precise fashion (Jola, 2006). Nevertheless, it cannot be anatomically correct, as the memory is shown to be located in the brain and not the muscles themselves. Hence the phenomenological experience is not matching the neurophysiological properties, which highlights the difficulty in capturing the elusive movement representations.

Remembering

In cognitive neuroscience, the term ‘motor program’ or ‘motor plan’ is used to explain how stored movements or movement patterns are represented. When learning a new movement, neurophysiological changes can be observed at different levels of the motor control system (see also chapter 4). A delay in the movement execution in imitation studies showed evidence that movements are stored even when only visually perceived (Meltzoff, 1995). However, it is not clear

whether a motor program exists for every single movement pattern or whether movements are chunked motor programs. Considering the neuronal aspects of storage, it is unclear at which levels the mechanisms are saved. It is generally agreed that the cerebellum plays a role in the fine control and coordination of movement performance (Martin, Keating, Goodkin, Bastian, & Thach, 1996). However, it remains unclear whether common motor control is at the level of modulation of motor neuron and muscle firing rates to control for movement parameters or whether movements were executed based on novel combinations of existing downstream elements (see Thach, Goodkin, & Keating, 1992).

It has also been suggested that movements might be represented by sequential ordered body representations (Head & Holmes, 1911) sometimes even negating a proper movement representation. Similar to cinematography, several following representations would elicit a sensation of movement. The functioning of Labanotation, a symbol language for notating dance, draws on this idea. In Labanotation, several body postures are indicated on a sheet of paper starting from the bottom to the top. When reading Labanotation, the symbols are transferred to a mental representation and a movement can be inferred by interpolating the following subsequent postures (see Experiment 3). Evidence for such a movement representation by combining static pictures is given by the apparent motion paradigm. Funk, Shiffrar, and Brugger (2005) found that a biologically plausible movement is perceived when participants perceived two alternating positions at a certain frequency. This apparent motion was observed even in impaired participants with an amputation of the corresponding limb. Thus an existing unconscious movement representation seems to define our visual perception of movements, but is it experienced by merging posture information?

Whether such sequential body representations show movement representation characteristics is a subject that has yet to be empirically supported.

Sensory Information

Clearly, as indicated above, a close connection between movement and body representation is likely based on sensory modalities: Afferent sensory information and motor action affect each other on a regular basis. For example, sensory afferent information plays an important role in motor learning. Also, it has also been shown recently that motor action unifies body limb representation (de Vignemont, Majid, Jola, & Haggard, 2009; Tsakiris, Prabhu, & Haggard, 2006). Therefore, movement representation holds as a basis for motor control where sensory afferents can be integrated, but is also adding to the sensory experience of the body.

The role of afferent information in motor control has been shown in several studies. For example, in a study with monkeys, the authors found that with the lack of afferent information only unfamiliar movements were severely impaired (Polit & Bizzi, 1979). Further, deafferented human patients were dependent on visual information for motor control (Cole & Sedgwick, 1992). Differences between visually or proprioceptively driven movements are not reflected in the fusimotor set (Vallbo & al-Falahe, 1990). Thus influence of afferent sensory information supports or substitutes any movement via movement representation. When a movement is familiar however, afferent information is less important; therefore, some movement sequences are possible in the absence of this peripheral feedback (Forget & Lamarre, 1987). Such movement representations therefore seem to cover the complete information necessary for a motor command. This is in accordance with Ghez, Gordon, and Ghilardi (1995),

who concluded that an internal model with the dynamic properties of the limb is required in both the planning and learning of movement. Such an internal model is taking into account that interaction torques act at different joints using proprioceptive information. Further, when proprioception is lacking, the internal model can partially substitute proprioceptive information within the internal model by vision of the limb in motion.

Moreover, movements are not only affected by sensory afferents from external events such as vision; there is evidence that mental processes such as motor imagery influence motor performance. Thus another way of looking at movement representation properties is to study the effects that internally generated processes have on the motor performance (chapter 4).

Mental Imagery

What is the functional neurological property of movement representation in motor control (for a review see Lotze & Halsband, 2006)? Jeannerod (1995) concludes that the neural substrates of conscious motor imagery share functionally equivalent neuronal processes with unconscious motor preparation. Lotze and Halsband, however, suggest that imagery has an important function not only in movement preparation but also in movement training. In correspondence with Lotze and Halsband the term 'movement representation', as it is used here, stands for more than mere movement preparation. Movement representation is handling motor plans, motor programs, movement commands (efferent information), bottom-up information from sensory signals (afferent information), as well as top-down information received from imagery, mental states, and visualisation processes.

The effects of mental and visual processes on movement representation in training are the subject of chapter 4. There is strong evidence for imagery training to increase movement performance (e.g., Yue, Wilson, Cole, & Darling, 1996; see also chapter 4). The relationship between imagery, movement representation, and actual motor actions is however unclear, and thus the effects of imagery on movement representation – in form of accessible motor programs – are investigated in that chapter. Is imagery just less than execution or is it something different in relation to movement representation? Clearly, a large number of studies have shown that motor imagery and motor executions share many anatomical substrates, but do not completely overlap. For an actual overview of current common neural activations for imagery and execution see Lotze and Halsband (2006). The experiment in chapter 4 is exceptional because it focuses on the training effects on a new nonestablished movement. This gives the opportunity to study the effect that mental processes have, when aspects of the movement representation are unsettled. In the current thesis, movement representation therefore stands for motor planning, motor program, and motor image.

Chapter Two

Body Representation in Response to Vision

Experiment 1: Mental Transformation of Objects and Bodies

Introduction

Mental imagery is often referred to as the ability to generate and manipulate mental representations of objects. Most studies on mental imagery use the mental object rotation task introduced by Shepard and Metzler (1971). This task requires the participant to decide whether two visually presented objects on the computer screen are the same or different. The greater the angular disparity between the two objects, the longer it takes the participant to respond. This finding was interpreted with the principle of transformational equivalence to real rotation of the object (Shepard & Cooper, 1982). However, mental rotation of objects is not the only task which requires the use of mental imagery. Different types of mental imagery are used to accomplish a variety of tasks (Hegarty & Kozhevnikov, 1999; Kosslyn, Brunn, Cave, & Wallach, 1984; Mast, Ganis, Christie, & Kosslyn, 2003; Mast & Kosslyn, 2002).

An important issue is the reference frame involved when we use mental imagery. The mental object rotation tasks (MORTs) as used by Shepard and Metzler (1971) require a transformation of the relation between the two objects while the viewer's position and perspective remain fixed. Other types of tasks,

however, are easier if people mentally change their own perspective and mentally rotate themselves (i.e., the representation of their body or body parts) rather than the objects. In this chapter, this type of task is referred to as the mental body rotation task (MBRT). In the MBRT, line drawings of human bodies are presented with one arm outstretched (e.g., Parsons, 1987a). The participant has to judge which arm of the figure is outstretched (left-right discrimination).

In everyday life, the abilities underlying the egocentric body transformation are used frequently in a variety of instances. For example, when we are in the office at work, we can visually imagine the policeman managing the traffic at the junction we just passed on our way to work. We can figure out in imagery whether the policeman was using the left or the right arm to signal the drivers when to go and when to stop. To extract more visual details from the imagined scene, we can mentally “zoom in” and thus will be able to discriminate smaller details. For example, we will then be able to judge whether the policeman was wearing glasses or not. Likewise, we can mentally “zoom out” to visualise the entire crossway so that we can judge in which direction the policeman was facing. Evidently, “zooming out” implies a change from small scale space to large scale space. The spatial context of the image becomes more relevant and is in fact needed for successful navigation. This example illustrates that the level of spatial resolution can be adjusted flexibly depending on the actual task. This is different from spatial perception, which is more or less bound to the physical properties of the immediate environment. Therefore, mental imagery is neither a large scale nor a small scale function. It seems that mental imagery operates widely independently of the spatial scale. The same principle may apply for perception where there may also be some constraints of small and large scale

spaces in imagery. Surprisingly, however, very few studies have been conducted on this topic (e.g., Malinowski, 2001). What are the spatial abilities necessary for mental operations in large scale space, such as navigation? In particular, perspective transformation turns out to be an essential strategy in navigation. One can take another person's perspective when that person, for example, asks for directions on how to get to a desired place of interest. This ability is noteworthy because it operates well in different spatial scales, in the immediately visible or tangible environment as well as in large scale space, outside our field of view. For example, we can mentally take the perspective of the Statue of Liberty just as well as the perspective of any normal-sized person.

In fact, there is support for the idea that MBRTs are a special class of mental spatial transformation, which – at least partially – rely on mechanisms separate from those responsible for MORTs. Strong evidence for the existence of two distinct components within spatial transformation processes is based on behavioural data. In contrast to the MORT, the reaction times in the MBRT showed no increase with angle of rotation (Zacks, Mires, Tversky, & Hazeltine, 2000). It is noteworthy, however, that there are also findings for the MBRT showing that error rates and reaction times depend on angular disparity even though the reaction times slopes were less steep than those reported for the MORT (see Parsons' Experiments 1 and 2, 1987a). Nevertheless, neuroimaging studies have revealed differences in brain activation when people are engaged in MORTs and MBRTs (Zacks, Rypma, Gabrieli, Tversky, & Glover, 1999; Zacks, Vettel, & Michelon, 2003). Moreover, an extrastriate body area in visual cortex revealed different activation when participants viewed body parts compared to nonbiological images (Reed & Farah, 1995).

The studies in this chapter further pursue the investigation of these two types of mental transformations. In particular, the MORT and the MBRT with exactly the same rotation conditions are compared. In fact, the MBRT requires the participants to make a perspective transformation in depth (i.e., z-axis) when the stimuli are presented in front view, facing the participant. However, when the stimuli are presented in back view (i.e., facing away from the participant) the participants can mentally rotate themselves in the picture plane (i.e., x-axis rotation) without any rotation in depth. Most studies using MORTs did not vary the axis of rotation. Therefore, the aim of the Experiment 1 was to compare the MORT and MBRT so that exactly the same geometry can be applied to perform the mental rotation. The rotation required to match the two cubes in the MORT corresponds with the rotation required to align the representation of one's body with the body stimuli in the MBRT. To the best of my knowledge, to date no study has yet been conducted comparing the MORT and the MBRT with the same rotation conditions within the same sample group.

Two mental rotation tasks

The reaction times (RTs) and the error rates (ERs) of two mental rotation tasks, a mental object rotation task (MORT) and a mental body rotation task (MBRT) were compared. The former was the classical Shepard and Metzler (Shepard & Metzler, 1971) cube rotation task with identical 3-D objects, and the latter was an egocentric body transformation task with body figures similar to those used by Parsons (1987a). In the MBRT the participants viewed schematic drawings of a body figure, which was presented under varying orientation conditions. The task was to judge which arm (i.e., left or right) of the body figure was outstretched.

The MBRT requires the viewer to transform the mental representation of his body to change the perspective in imagery. No perspective transformation was required for the MORT as the mental transformation of one or both objects can be performed without changing one's own perspective.

In previous studies using the MBRT or the MORT, none of the rotation conditions were matched properly. Therefore, the two tasks were designed with corresponding rotation axes and angles of rotation. This means that identical angles were used to match the two cubes in the MORT and to match the representation of one's body to the body figure on the computer screen in the MBRT. In the classical mental rotation task, the response in the MORT is supposed to show a significant increase with increased rotation of the angle in the plane (i.e., x-axis rotation). When the stimuli are also rotated in depth (z-axis rotation), additional mental transformation costs are assumed, thus leading to increased reaction times. These results will be compared with the MBRT. A similar increase in reaction time for the MBRT would not corroborate the assumption of distinct mental rotation mechanisms underlying the MORT and the MBRT. Alternatively, however, if the results revealed clear differences between MORT and MBRT, it would speak for a potential dissociation.

Method

Participants

Twenty-two participants, 13 female and 9 male, volunteered to participate in the experiment, of which 36.4% had a university degree, 54.5% had attended a comprehensive secondary school. The mean age was 27.6 ± 4.9 years. All participants gave their informed consent in a verbal agreement.

Materials

Two different sorts of stimuli were presented for each task: line drawings of human bodies for the MBRT and cubes for the MORT. Both types of stimuli could appear rotated in depth (0° vs. 180°) and rotated in plane (0°/45°/90°/135°/180°). For the MBRT the stimuli were similar to those used by Parsons (1987a). The stimuli in the cube rotation task were the classical figures used by Shepard and Metzler (1971).

Task and Procedure

The participants were tested in two tasks (MBRT and MORT) individually in a quiet room. Before the experiment started, handedness was assessed by means of a questionnaire (Briggs & Nebes, 1975). The instructions to the tasks were standardised and participants read them on their own. The participants underwent a training session with 10 test trials in order to become familiarised with the task and the stimuli. If the error rate in the test trials was higher than 30% the training session was repeated.

In the MBRT, 40 schematic line drawings of human bodies (see Figure 2, p. 46) were presented on a 12.1" apple computer screen (viewing angle 15.7°). The stimuli were rotated clockwise in 5 different plane rotations (0°/45°/90°/135°/180°) and 2 different depth rotations (0° vs. 180°), making a total of 10 possible rotation conditions. In 50% of the trials the right arm was outstretched and in the other 50% the left arm was outstretched. Thus, each rotation condition was presented with the left and the right arm, crossed and uncrossed, each repeated 6 times, making a total of 240 trials. The participants were seated upright facing the computer screen and had to judge whether the left or the right arm of the human body figure was outstretched, using the index finger

of the corresponding arm. In the examples (a) and (b) illustrated in Figure 2 (p. 46), the participant would use the index finger of the left hand for a correct answer. Accordingly, the participants responded with the index finger of the same arm they indicated and imagined as outstretched. The use of crossed and uncrossed arms discouraged the use of learning strategies based on the visual appearance of the stimuli (e.g., the use of a strategy like “if the stimulus appears in front view, then push the button opposite to the side of the outstretched arm” for stimuli presented at 0°). That is, for 50% of the upright stimuli the corresponding arm was not on the same side (e.g., front uncrossed and back crossed). Therefore, the participants were encouraged to perform an egocentric body rotation to give the correct answer.

The MORT was a same-different paradigm with same or mirror-reversed cubes presented in adjacent locations (left side and right side of the screen). Half of the trials were same trials, the other half were different trials. The task was to decide whether the two cubes presented simultaneously on the computer screen were the same or different. The cubes were presented in exactly the same 10 possible rotation conditions as the line drawings of the human bodies (i.e., 5 different rotation angles clockwise in the plane, 0°, 45°, 90°, 135°, and 180°; and 2 different rotation angles in depth, 0° and 180°). As in the MBRT, the two planes of rotation were combined, so that, unlike in the Shepard and Metzler paradigm (Shepard & Metzler, 1971), a cube could be rotated in plane and in depth. Therefore 10 possible rotation conditions were tested; with the stimuli either presented with the mirror-reversed cube or the original, either with the zero rotation cube (i.e., 0° plane rotation, 0° depth rotation) on the left or on the right

side in either the same or different condition. Each condition was repeated 3 times, making a total of 240 trials.

For the experiment proper, the total of 240 trials in each task were divided into three blocks. Each of the 40 combinations in the MBRT (e.g., 90° plane rotation, 180° depth rotation, arms crossed) was presented 2 times in a block. The order of the blocks and the order of the trials within the blocks were pseudo-randomised (i.e., the same combination did not occur more than twice in succession). There was no time limit for the two tasks. Between the blocks, a short break allowed the participants to stretch their fingers and relax their eyes.

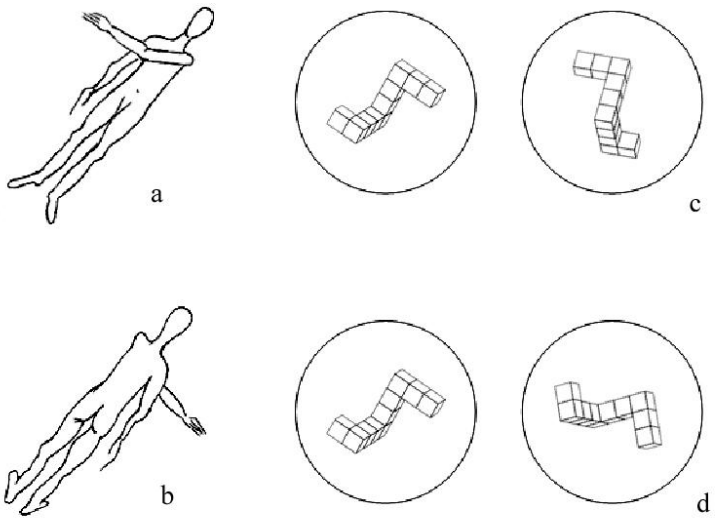


Figure 2. Examples of stimuli in the 45° plane rotation condition of the MORT and the MBRT of Experiment 1. (a) and (b): examples of MBRT with one stimulus in (a) 180° depth and 45° plane rotation and (b) 0° depth and 45° plane rotation from the observers' upright position. (c) and (d): examples of MORT with two stimuli in (c) 180° depth and 45° plane rotation and (d) 0° depth and 45° plane rotation from each other.

After each task, the participants were asked about their strategies and about any difficulties they experienced while solving the tasks. Moreover, they filled out three questionnaires translated into German; the VVIQ (Vivid Visual Imagery

Questionnaire, Marks, 1973), the SUIS (Spontaneous Use of Imagery Scale Kosslyn, Shepard, Thompson, & Chabris, n.d.), and the VMIQ (Vividness of Movement Imagery Questionnaire, Isaac, Marks, & Russel, 1986). The scale of the VMIQ was inverted in order to match with the scale of the VVIQ (i.e., 5 for the *highest* imagery rating and 1 for the *lowest* imagery rating). Only self-ratings of the participants that could be analysed in both tasks were averaged.

Analysis

The values in the text are given as mean (*M*) ± standard deviation (*SD*) in milliseconds for the reaction times (RTs) and in percentages for error rates (ERs). In figures, deviation is indicated by standard error (*SE*). Only RTs from correct trials were used. Trials with RT values greater than *M* ± 3.0 x *SD* were defined as outliers and therefore excluded from the data analysis. These trials were less than 4% of all correct answers for each participant. Participants with ERs higher than 25% were excluded from data analysis. Up to 50% of their correct and false responses were presumably produced by guessing. For the MBRT, participants with ERs higher than 10% (e.g., *M* ± 2.5 x *SD*) were excluded because this task was easier than the MORT.

Effects of plane rotation and depth rotation were analysed. As the MORT and the MBRT have not been matched for difficulty, they were analysed separately. Descriptive data, ANOVAs with the factors plane rotation (0°/45°/90°/135°/180°) and depth rotation (0° vs. 180°), deviation contrasts and Bonferroni post-hoc *t* tests were computed. Furthermore, two-tailed weighted (polynomial) contrasts were used to test for linear trends. In the MBRT, the rotation angles were defined with respect to the participant. Therefore, the body figures presented in back view were defined as 0° depth rotated, whereas the

body figures presented in front view were defined as 180° depth rotated. In the MORT, rotation angles were defined by the angle between the two cubes.

Results

Three participants had to be excluded from data analysis in the MORT. Two had more than 25% ERs and the RTs of one exceeded 30 s in 18.3% of the correct trials. All participants were included in the MBRT. Mean scores of ERs and RTs were higher for the MORT than the MBRT as listed in Table 1 (p. 48).

ERs and RTs for all rotation conditions are illustrated in the Figure 3 and 4 (p. 51). A repeated measures ANOVA for ERs with the factors plane rotation and depth rotation revealed significant main effects in the MORT for both factors plane, $F(4, 72) = 20.63$, $p < .001$, and depth, $F(1, 18) = 14.32$, $p < .01$. The factors plane and depth did not interact, $F > 1$. In the MBRT, the repeated measures ANOVA of ERs showed a main effect for the factor plane, $F(4, 84) = 3.70$, $p < .01$. The factor depth showed no main effect. There is, however, a significant interaction with the factor plane, $F(4, 84) = 5.87$, $p < .001$.

Table 1.

Mean Error Rates in % and Mean Reaction Times in Milliseconds (±SD) for Dancers (see Experiment 2) and Nondancers of Experiment 1 in both Mental Rotation Tasks.

	Mental Object Rotation		Mental Body Rotation	
	$Dancers_a$	$Nondancers_b$	$Dancers_c$	$Nondancers_d$
Error Rates	11.8 ± 5.67	12.4 ± 6.38	1.6 ± 1.84	2.2 ± 2.29
Reaction Times	6791 ± 2447	5002 ± 1963	1453 ± 715	1280 ± 484

Note. $^a n = 20$. $^b n = 19$. $^c n = 24$. $^d n = 22$.

ERs in the depth rotation condition are higher for angles less than 90° in the MORT and the MBRT (illustrated in Figures 3 and 4, p. 51). For plane rotations above 90°, stimuli with no depth rotation were more difficult in the MBRT. As the ERs in the MORT (see Figure 3, p. 51) showed an interaction at 90° too, linear contrasts were computed for nondepth rotated and depth rotated stimuli separately as well as paired t tests (depth rotated vs. nondepth rotated stimuli) for both tasks, although the factors plane and depth did not interact in the ANOVA that was computed for the MORT.

For RTs, the repeated measures ANOVA revealed a significant main effect of the actor plane, with longer RTs for increasing rotation angle in both the MORT, $F(4, 72) = 24.88$, $p < .001$, and the MBRT, $F(4, 84) = 36.85$, $p < .001$. The factor depth rotation is significant with longer RTs for depth rotated cubes only, $F(1, 18) = 52.22$, $p < .001$ (MORT). The two factors plane and depth rotation interacted in both the MORT, $F(4, 72) = 8.42$, $p < .001$, and the MBRT, $F(4, 84) = 28.47$, $p < .001$.

Linear trend analysis for the MORT revealed longer RTs with increasing plane rotation without depth rotation, $t(90) = 5.78$, $p < .001$, and with depth rotation, $t(90) = 2.32$, $p < .05$. The same analysis for nondepth rotated body figures revealed significantly longer RTs with increasing plane rotation, $t(105) = 7.33$, $p < .001$, and a significant quadratic trend, $t(105) = 3.42$, $p < .01$. The RTs for depth rotated body figures showed neither a linear nor a quadratic trend.

Paired Bonferroni post-hoc comparisons (see Table 2, p. 50) for the MORT showed that depth rotated cubes have significantly longer RTs than nondepth rotated cubes for all plane rotation conditions except for 180° plane

rotation where the depth rotation showed no significant effect. Comparisons between front and back oriented body figures revealed significantly longer RTs for front bodies for all plane rotations below 135°. As can been seen in Figure 4 (p. 51), front bodies showed shorter RTs when the body figures were inverted.

Independent samples *t* test for mean ERs in percentages of female participants, *M* = 11.0 ± 5.4 (MORT) and *M* = 2.2 ± 2.1 (MBRT), versus male participants, *M* = 13.9 ± 7.4 (MORT) and *M* = 2.1 ± 2.8 (MBRT) revealed no gender difference. Moreover, an independent samples *t* test did not reveal significant differences in RTs between female, *M* = 5206 ± 2486 (MORT) and *M* = 1260 ± 530 (MBRT) and male participants, *M* = 4775 ± 1267 (MORT) and *M* = 1310 ± 438 (MBRT).

Table 2.

Analysis Sample of Paired Contrasts for the Type of Rotation in Depth (0° vs. 180°) in Mean Reaction Times in Milliseconds and Error Rates in % (±SD) of Experiment 1 with T- and p-Values (column right of measure).

	Reaction Times	T-Value	Error Rates	T-Value
		Mental Object Rotation$_a$		
0º	-1935.8 ± 1179.4	7.15***	8.95 ± 12.01	3.25**
45º	-1244.9 ± 945.2	5.74***	7.33 ± 14.18	2.25*
90º	-1425.6 ± 1227.1	5.06***	-.34 ± 15.19	-0.10$^{n.s.}$
135º	-812.3 ± 1304.9	2.71*	7.82 ± 13.03	2.62*
180º	-66.5 ± 1062.5	0.27$^{n.s.}$	9.08 ± 16.65	2.38*
		Egocentric Body Transformation$_b$		
0º	-422.3 ± 279.6	7.08***	2.39 ± 3.25	3.45**
45º	-348.4 ± 274.4	5.95***	1.96 ± 4.73	1.94†
90º	-154.5 ± 218.2	3.32**	.43 ± 5.26	0.38$^{n.s.}$
135º	22.2 ± 310.0	-0.34$^{n.s.}$	-1.76 ± 3.67	-2.25*
180º	774.4 ± 726.3	-5.00***	-3.96 ± 6.93	-2.68*

Note: ^{a}n = 19. ^{b}n = 22. $^{\dagger}p$ < .07. *p < .05, two-tailed. **p < .01, two-tailed. ***p < .001, two-tailed.

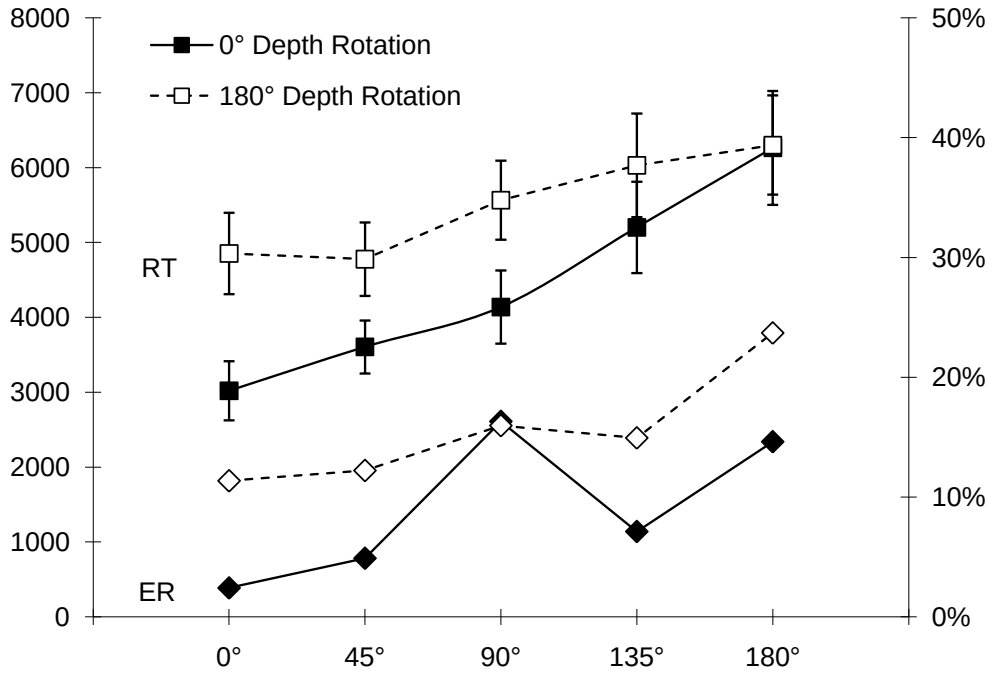


Figure 3. Participants' performance in the mental object rotation task in Experiment 1 (n = 19). Please see caption Figure 4 for axis measures and further figure explanations.

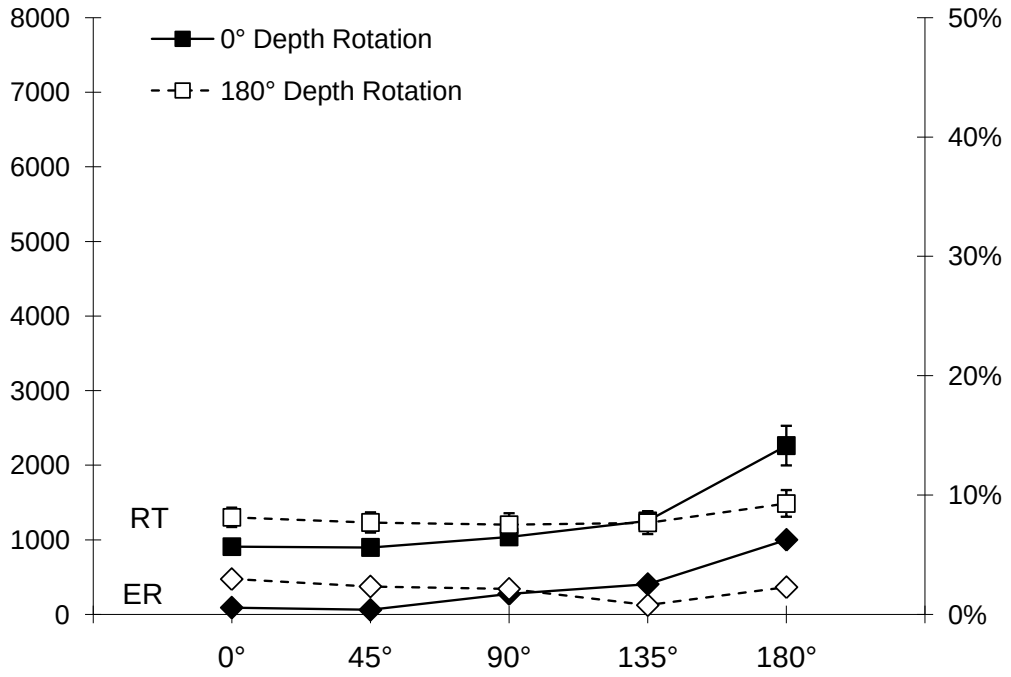


Figure 4. Participants' performance in the mental body rotation task in Experiment 1 (N = 22). Data are shown for 0º (black squares) and 180º (white squares) depth rotation in all plane rotation conditions in means (±SE); x-axis: degrees of plane rotation; y-axis (left scale): reaction times in milliseconds; y-axis (right scale): error rates in %.

Mean scores for each of the two parts of the VMIQ (imagine oneself moving and imagining seeing someone else moving), for the VVIQ, and for the SUIS are listed in Table 3 (see column for nondancers, p. 52). The two parts of the VMIQ differed significantly in a paired *t* test, $t(17) = 2.65$, $p < .05$. There was a strong significant positive correlation between each of the two parts of the VMIQ and the VVIQ, r = .867, $p < .001$ (imagine oneself moving) and r = .893, $p < .001$ (seeing someone else moving). The SUIS showed no correlation with any of the two other questionnaires. However, it revealed a significant correlation with the RT and the ER of the MORT, r = 0.40, $p < .05$ for RT, and r = 0.41, $p < .05$ for ER. The RT of the MORT and the RT of the MBRT showed a significant correlation, r = 0.52, $p < .05$.

Table 3.

Mean Scores of the Imagery Questionnaires of Experiments 1 and 2 (±SD), Chi-square, and p-Value.

	Dancers[a]	Nondancers[b]	χ^2[c]
VMIQ, part 1	96.7 ± 23.8	90.3 ± 16.2	3.56[†]
VMIQ, part 2	99.9 ± 15.4	99.5 ± 14.6	.01
VVIQ	65.5 ± 7.6	63.7 ± 8.4	.51
SUIS	41.8 ± 7.9	37.4 ± 9.2	2.18

Note: Three participants of the nondancers group and eight participants of the dancers group were excluded due to their error rates and reaction times (see Experiments 1 and 2). Also, one participant of the nondancers group with an average daily physical training comparable with that of dancers was excluded. VMIQ = Vividness of Movement Imagery Questionnaire (maximum score 120 for each part). Part 1 = imagine somebody else. Part 2 = imagine oneself. VVIQ = Vivid Visual Imagery Questionnaire (maximum score 80). SUIS = Spontaneous Use of Imagery Scale (maximum score 60). [a]$n = 19$. [b]$n = 18$. [c]df = 1, $N = 37$. Kruskal-Wallis H-test: [†]$p < .07$.

Discussion

The results show that the MORT is more difficult than the MBRT. The participants made more errors and it took them longer to respond. The high ERs found in the MORT were comparable to those of other studies using cubes rotated in depth and in plane (Jordan, Heinze, Lutz, Kanowski, & Jäncke, 2001). Moreover, it has to be noted that the participants in other studies used extensive amounts of practice over the sessions. For example, Shepard and Metzler (1971) used 1600 pairs divided into blocks of about 200, which were tested in 8 to 10 one-hour sessions. The pattern of the ERs in the MORT showed an increase in task difficulty with increasing angular disparity as revealed by other studies (Kosslyn, Thompson, Wraga, & Alpert, 2001; Wraga, Thompson, Alpert, & Kosslyn, 2003). The ER was higher for cubes rotated in depth than for cubes rotated in plane only. For the MBRT, however, the orientation of the body figures (back view or front view) interacted with rotation angle. ERs increased with increasing angle when the body figures were seen in back view whereas the ERs remained flat for all angles when the body figures were seen in front view.

The analysis of RTs in the MORT shows the typical increase in RT length with increasing angular disparity reported by Shepard and Metzler (1971). This finding has also been confirmed by more recent studies (e.g., Jordan et al., 2001; Kosslyn, DiGirolamo, Thompson, & Alpert, 1998; Kosslyn et al., 2001). A new finding reported in this study is the linear relationship we found for cubes which were rotated in depth and in plane. Shepard and Metzler measured the two axes separately without combining the two rotations. In the MBRT, the RTs for body figures rotated in depth (the body figure is seen in front view) did not vary as a function of rotation angle. This result confirms earlier findings by Zacks

et al. (2000) who presented figures in front view only. However, the RTs increased with increasing angle when the stimuli were presented in back view. How can we explain this difference? It is possible that participants make a shortest path rotation when the body figures are rotated in depth. Parsons (1987a, Experiment 1) suggested that the shortest path accounts for about 50% of the variance. The idea of a shortest path rotation is supported by the inverse contrast in RT found for upside down body figures. The RTs were shorter when the figures were rotated in depth. It is assumed that the orientation of an upside down figure is reinterpreted and therefore viewed as someone lying on their back (i.e., supine). In fact, several participants described some sort of kinesthetic experience when they solved the task with upside down figures presented in front view. A few participants reported that they mentally rotated themselves backward (similar as if they were slipping on a banana peel). Therefore, no mental rotation around the longitudinal axis (depth rotation) is required to solve this particular condition. Interestingly, we found a similar pattern in the MORT. The RTs were shorter at 180° when the cubes were also rotated in depth. Even though this difference did not reach statistical significance it could be related to Murray's (1997) finding, which demonstrated the advantage of a strategy to mentally flip an inverted natural object rather than rotating it along the picture plane.

Contrary to other studies showing gender differences in mental rotation tasks (Emmorey, Klima, & Hickok, 1998; Linn & Petersen, 1985; Peters et al., 1995), no significant effect of gender was evident in this study. Also, no advantage for participants with high mental imagery scores could be found (VVIQ, VMIQ) with the only exception being the SUIS, which correlated with performance in the MORT (shorter RTs and lower ERs).

The idea that people used different strategies motivated further testing on another group of participants. Unlike other studies, in which the strategy was primed via instruction (e.g., Kosslyn et al., 2001), the current study investigated expertise and its possible role in acquiring different cognitive strategies. The aim was to compare experts with nonexperts to study possible differences in the mechanisms that underlie the MORT and the MBRT.

Summary

An important question in studies on mental rotation is whether the mental rotation of objects (Shepard & Metzler, 1971) and the mental transformation of bodies (Parsons, 1987a) rely on dissociable mechanisms. Most studies support the assumption that the two tasks are different either due to the task specificities (discrimination vs. identification) or due to the stimuli (cubes vs. body drawings). However, the rotation angles in most of these studies were not matched between the two tasks. Therefore, in this experiment, the cubes and body figures were presented in exactly the same rotation conditions in order to provide identical transformation processes; in the picture plane, 0°, 45°, 90°, 135°, and 180°, and in combination with a rotation in depth, 0° (the stimuli are rotated in the picture plane only) and 180°. A linear increase in RTs with increasing angle for the cubes could be replicated, whereas the RTs for rotated body figures increased only when they were presented from the back (nondepth rotated bodies). However, the RTs for inverted body figures were shorter when they were rotated in depth (front view) compared to when they were rotated in the picture plane only (back view). This finding suggests that participants use different strategies depending on the perceived orientation of the stimulus. This finding suggests that

participants use different strategies depending on the perceived orientation of the stimulus.

The results do not support the assumption of a clear difference between the mental rotation of objects and bodies. However, it can be suggested that the orientation of the visual stimuli defines the angle of mental rotation. In order to validate the influence of motor and visual experience, the same tasks were performed by dancers as experts in the following Experiment 2. If the orientation of the visual stimuli is a defining property of the mental rotation process, then motor experience may be beneficial to solve the task. Several studies have shown that the motor system is closely connected with mental representation processes (e.g., Wexler, Kosslyn, & Berthoz, 1998). Therefore, movement experts would be expected to show an advantage in general or for particular rotation angles only. Else if the representation form of the visual stimulus is responsible for differences in mental transformation processes, then visual experience may be beneficial. Dancers who are experienced in observing and representing moving bodies would be expected to show a body transformation advantage.

Experiment 2: Effects of Expertise on Mental Transformation

Introduction

The performance of a second group of participants was tested in the identical tasks as described in Experiment 1. The aim was to study the influence of expertise on performance in the mental object rotation task (MORT) and in the

mental body rotation task (MBRT, see Experiment 1 for further information on the tasks). If the two tasks share the cognitive processes involved in mental transformation, we would expect a group with expertise in one task (i.e., mental rotation of bodies) to show a transfer effect and perform better in both tasks. If, however, the processes involved in the MBRT are – to some extent – different from those involved in the MORT it is possible that expertise is bound to only one of these tasks and therefore does not influence performance in the other task.

Differences in expertise for mental imagery tasks were reported in several studies. For example, pilots (Dror, Kosslyn, & Waag, 1993), athletes (Ozel, Larue, & Molinaro, 2002), and men (Jordan et al., 2001; Jordan, Wüstenberg, Heinze, Peters, & Jäncke, 2002) are faster in MORTs. Several authors suggest a correlation with sport or gymnastic expertise (e.g., Creem, Wraga, & Proffitt, 2001), but until now, no expertise effect has yet been published for the MBRT.

In this comparison professional dancers were recruited as experts. Overby (1990) found significant differences in imagery tests (i.e., body image, cognitive imagery, and spatial imagery) between experienced dancers and novices. He postulated that it is the dancers' physical manipulation of space which enhances their ability in visuo-spatial concepts. Moreover, dancers learn through external feedback via the mirror and from the instructors. Therefore, they acquire a lot of practice in real and imagined body transformations. For example, Ramsay and Riddoch (2001) found greater accuracy for ballet dancers in a position-matching task of the upper limb. Several studies on body representation and sensorimotor perception have demonstrated improved proprioceptive discrimination abilities in professional dancers and other athletes (e.g., Barrack, Skinner, & Cook, 1984). Taken together, we expected dancers to perform better

in the MBRT as a result of their training in mental imagery, kinesthetic experience, and postural control. Furthermore, if the MORT and the MBRT share mental rotation processes, then the effect of expertise should have a benefit on both tasks. The aim was to compare the results we described above (nonexperts) with a matched expert group which therefore should differ in their expertise of movement only.

Method

Participants

An expert group of 27 professional dancers or dance students (14 female dancers, 13 male dancers) were matched by age and gender to the sample of Experiment 1. Informed consent was given by all participants in form of verbal agreement. The dancers performed the same tasks as the nondancers (participants of Experiment 1). The sample criterion for the dancers was that they currently work or study as a dance performer, teacher, or choreographer or as a high level dance manager in a field such as ballet, modern dance, contemporary dance, or jazz dance. They have had at least 1 hour of coordinative dance training per day over the last 5 years (defined as coordinative training per day). The mean age of the dancers was 30.5 ± 6.8 years. They were given the same instructions as the participants in the previous study (Experiment 1). Regarding education, 37% of the dancers have a university degree, 40.7% completed a comprehensive secondary school. The average training time per day was 213 ± 120.2 min and the amount of training per day was normally distributed, df(17) = 0.94, p = .30 (Shapiro-Wilk test). None of the dancers had participated in any mental rotation experiment prior to this study.

Materials, Design and Procedure

The materials and tasks, the questionnaires, and the procedure, as well as the data analysis and participants exclusion criteria are identical to the experiment described above (Experiment 1). The analysis differs in the additional between-subjects factor expertise (dancers vs. nondancers) and the supplementary testing of the factor spatial compatibility in the MBRT (compatible vs. incompatible). To conduct these between-subjects analysis properly, the two independently measured samples (dancers and nondancers) had to be matched except for their expertise of movement. The expertise of movement was defined as the daily training time in coordinative dance training or other forms of coordinative training over the last 2 years.

Results

In the following paragraph, the results were outlined for the effect of dance expertise in reaction times (RTs) and error rates (ERs) in the MORT and the MBRT. For comparison, the data from the nondancers (Experiment 1) are included in the figures. Three female dancers and 4 male dancers with more than 25% ERs had to be excluded from data analysis in the MORT. Two of them and an additional female dancer had ERs higher than 10% in the MBRT.

It is noteworthy that the average training time per day for the nondancers of the 1st sample differs significantly from a normal distribution, df(22) = 0.731, $p < .001$ (Shapiro-Wilk test). One participant from the nondancers group exceeded the average training time per day by three standard deviations ($M \pm 3.0$ x *SD)*. This participant was excluded from comparison. It was considered that his high expertise in snowboard jumping, and therefore heightened spatial awareness, could be compared to a dancers' expertise. A nonparametric H-test

for a comparison between the dancers and the nondancers indicated that the groups differed significantly in the amount of coordinative training, M = 3.52 ± 2.01 for the dancers versus M = 0.35 ± 0.47 for the nondancers; $\chi^2(1, N = 27) = 32.45$, $p < .001$ (Kruskal-Wallis). However, age, gender, and education did not differ between dancers and nondancers.

The responses for the experts are illustrated in Table 1 (p. 48). In the MORT, the ANOVA with the between-subjects factor expertise (dancers vs. nondancers) with the within-subjects factors plane and depth rotation revealed a significant effect of expertise in reaction time (RT), $F(1, 36) = 7.43$, $p < .05$, and a trend for interaction between the factors expertise and plane rotation in the ER, $F(4, 144) = 1.57$, $p = .185$. The mean RTs and ERs for the MORT are illustrated below in Figure 5 (p. 62) which shows shorter RTs of the nondancers compared to the dancers. The same trend with shorter RTs of the nondancers compared to the dancers in the MBRT is visible in Figure 6 (p. 62), although no significant main or interaction effect of expertise in the MBRT could be found.

In the MORT, the factors plane and depth rotation showed significant main and interaction effects in RT, $F(4, 144) = 55.9$, $p < .001$, for plane, $F(1, 36) = 155.91$, $p < .001$, for depth, and for the interaction between plane and depth, $F(4, 144) = 16.8$, $p < .001$. Significant main and interaction effects were found in ERs for plane, $F(4, 144) = 40.36$, $p < .001$, depth, $F(1, 36) = 19.78$, $p < .001$, and the interaction between plane and depth, $F(4, 144) = 7.76$, $p < .001$. In the MBRT, the factor plane revealed a significant main and interaction effect in RT for the factor plane, $F(4, 140) = 61.5$, $p < .001$, and for the interaction between plane and depth, $F(4, 140) = 51.23$, $p < .001$. The factor depth showed no significant main effect in RT in the MBRT. In the ERs, the factor plane showed

a significant main and interaction effect, $F(4, 172) = 8.2$, $p < .001$, for plane, $F(4, 172) = 11.07$, $p < .001$, for the interaction of plane and depth. Depth showed a tendency for a main effect in ER only, $F(1, 43) = 3.23$, $p = .079$. As the separate analysis of the dancers sample revealed similar results as reported above for the nondancers they are not addressed in more detail here.

It could be shown in choice RT tasks that how long it takes participants to respond depends on the spatial relationship between stimulus and response. According to the spatial compatibility effect, the RT is slowed down if the stimulus side is not compatible with the side of the requested response (Simon & Rudell, 1967). In the MBRT participants made compatible conditions (e.g., stimulus pointing to left and for a correct answer the participant had to respond with the left hand) and incompatible conditions (e.g., stimulus pointing to the left and for a correct answer the participant had to respond with the right hand). For example, for upright body figures in back view the responses were spatially compatible when the arms were presented uncrossed. An analysis for the compatibility effect with the factors plane and compatibility showed significant main effects for both factors compatibility, $F(1, 43) = 87.79$, $p < .001$, and plane, $F(1, 43) = 82.17$, $p < .001$. Moreover, the two factors plane and compatibility interacted, $F(1, 43) = 16.56$, $p < 0.001$. Paired post-hoc Bonferroni t tests for spatially compatible versus spatially incompatible stimuli revealed that RTs for incompatible stimuli are longer at 0° plane rotation, $t(21) = 5.50$, $p < .001$, and at 180° plane rotation, $t(21) = 5.32$, $p < .001$.

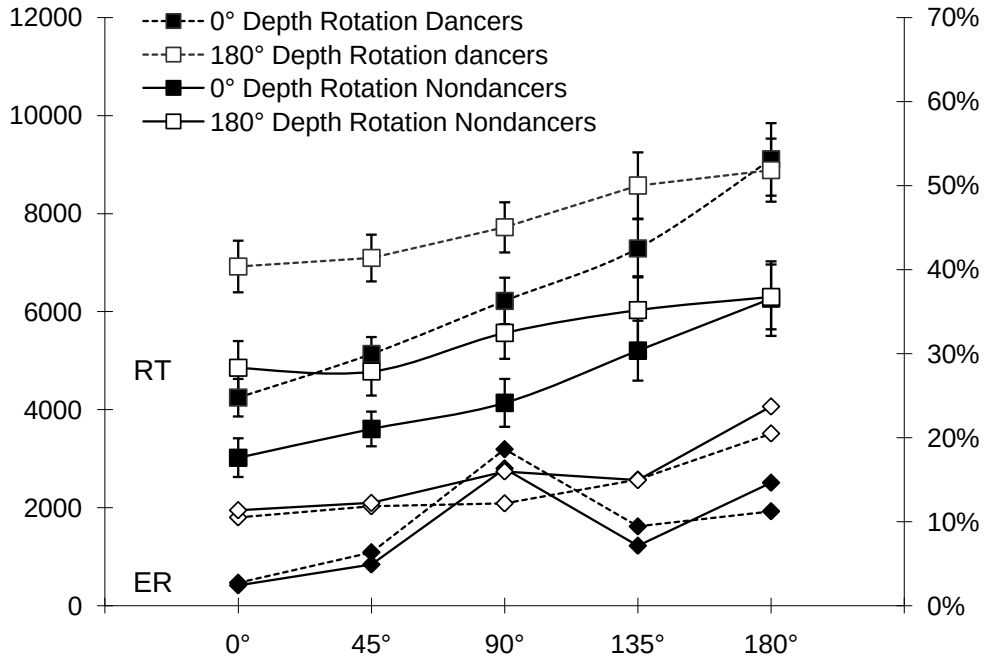


Figure 5. Dancers' versus nondancers' performance in the mental object rotation task in Experiments 1 and 2 (n = 20 and n = 18, respectively). Please note that the y-axis scales differ from Figure 6 below. Please see caption Figure 6 for axis measures and further figure explanations.

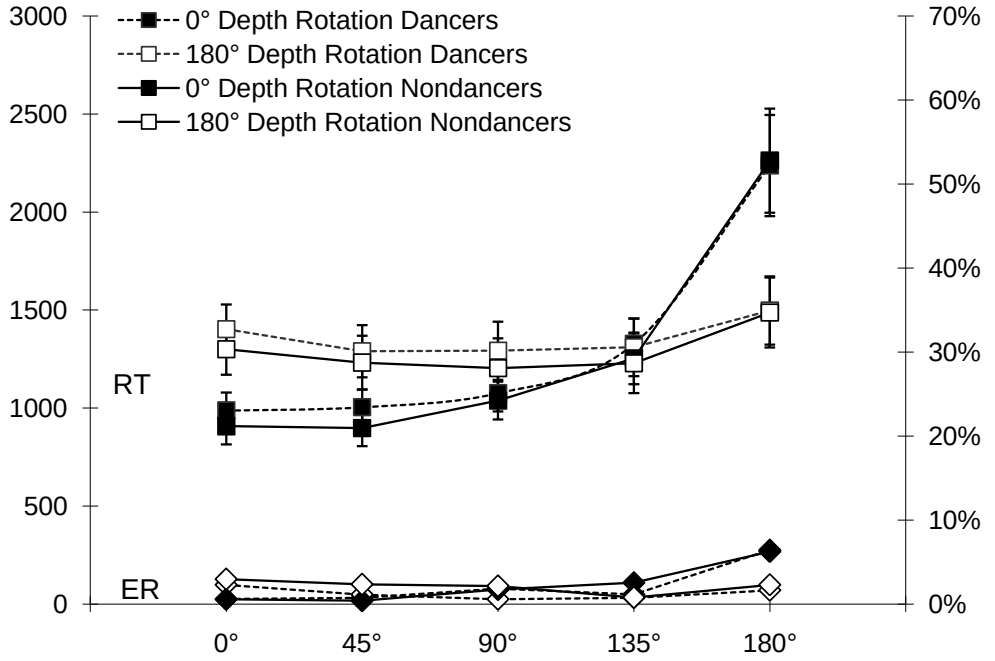


Figure 6. Dancers' versus nondancers' performance in the mental body rotation task in Experiments 1 and 2 (n = 19 and n = 18, respectively). Data are shown for dancers (dotted lines) and nondancers (bold lines); for 0º (black squares) and 180º (white squares) depth rotation in all plane rotation conditions in means (±SE); x-axis: degrees of rotation; y-axis (left scale): reaction times in milliseconds; y-axis (right scale): error rates in %. Please note that the scales differ from Figure 5 above.

Discussion

This study pursued two aims. The first aim was to compare the MORT and the MBRT with exactly the same rotation conditions. Previous studies compared behavioural and neuroimaging data with unequal rotation conditions (Jordan et al., 2001; Zacks et al., 2000). The second aim was to compare professional dancers' performance to the performance of nondancers in the MBRT and MORT. In particular, dancers were expected to perform better in the MBRT.

Consistent with many other studies on the mental cube rotation task, a linear increase in RT with increasing angle rotation was found. One of the new findings reported in this study is the linear positive relationship we found for the RTs in the MORT when the cubes are rotated in depth and in plane simultaneously. Shepard and Metzler (1971) measured the two axes separately without combining the two rotations. The additional time for depth rotated cubes was required for all plane rotation conditions except for the upside down stimuli, where the difference between depth rotated and nondepth rotated cubes did not reach significance. It is probably the case that participants used a more direct path for the inverted cubes (e.g., like flipping the objects as described by Murray, 1997), and thus they were able to save some processing time in contrast to the 180º plane rotation.

The comparison between the body figures presented in front view and in back view is more difficult. The RTs and ERs were both constant for all plane rotation conditions when the stimuli were presented in front view, whereas they increased with increasing angle for back view stimuli. It is not clear whether the participants actually perform a mental rotation when they are exposed to body stimuli presented in the front view. It is possible that they use a totally different

strategy since the behavioural data for the front view stimuli are not dependent on rotation angle. This is similar to other studies that have shown that a spatial inference in mental environments does not depend on the direction of the body to the object (e.g., Franklin & Tversky, 1990). It is therefore possible that the different results for body figures presented in front and back view imply a change in scale; from small scale for back view to large scale in front view. However, based on the behavioural data, it may be more appropriate to limit the comparison between MBRT and MORT to the back view body figures and the cubes rotated in plane only. In both cases, RTs depend on rotation angle and the geometry of the mental rotation is matched. An extension of the results showing the difference between front-view and back-view body figures would clearly be desirable. As far as the results indicate, the stimuli rotated in plane only show the same pattern for both types of tasks while the behavioural responses differ when the cubes and the bodies are also rotated in depth. It remains a hypothetical question whether the perspective transformation necessary for the body figures rotated in depth is the only reason for this difference.

Interestingly, in the MBRT, the RTs were shorter for upside down body figures in front view (facing the observer) than for upside down body figures in back view. The front view stimuli were thought to require an additional transformation since they were rotated in depth with respect to the participants. However, the participants may have chosen the shortest path when they rotated themselves mentally (Parsons, 1987a). This is possible because the stimulus could be viewed in two alternative ways; as a figure rotated 180° in plane and 180° in depth (i.e., upside down) or as a figure lying on the back (resting in the supine position). Several participants reported after the experiment that they have

viewed the 180° stimuli not upside down but rather in the supine position. This suggests that they mentally rotated the representation of their body backward to solve the task. The fact that some participants verbally reported the strategy they used for solving the task (i.e., they mentally rotated themselves backward) is not yet conclusive regarding the mechanisms that underlie their responses.

It is noteworthy that no increase of RTs was found in the MORT when inverted cubes were rotated in depth. In this context, it is interesting that Parsons (1987a, part C in Experiment 2) revealed a linear increase for body figures in front view presented within a surrounding environment. Parsons' finding suggests that the participants are no longer able to reinterpret the orientation of the stimulus (they then view it upside down instead of lying on the back). In addition, it is noteworthy that there is a spatial compatibility effect involved in this result. If for example participants identify the outstretched arm (crossed or uncrossed) close to the body (e.g., at the height of the shoulder), correct answers are spatially compatible for the upside down body figures in front view whereas correct answers for upside down body figures in back view are spatially incompatible. Future studies need to separate these two possible explanations.

In this chapter, expertise effects were investigated in comparing dancers and nondancers. Even though there was no effect of expertise in the expected direction (dancers' performance was not better in the MBRT), there was a significant difference between dancers and nondancers in the MORT. Contrary to Ozel et al. (2002) who found improved performance in mental object rotation for sport experts like gymnasts, the dancers were in fact slower than the nondancers in here. The dancers' impaired performance (longer RTs) in the MORT could be due to the fact that they were trying to apply a different strategy to solve the task.

Some of the dancers reported that they tried to rotate themselves mentally to align with the cubes they saw on the screen. This may have resulted in a more complex perspective transformation. Therefore, it is possible that their experience led to an inappropriate strategy and thus interfered with task performance in the MORT. Despite the fact that dancers have improved abilities in the perception of postures (Euzet & Gahéry, 1996), a more accurate proprioceptive discrimination (Barrack et al., 1984), and a stronger body representation (Ramsay & Riddoch, 2001), the MBRT did not show any effect of expertise. The lack of expertise effects between the dancers and the nondancers in the MBRT may have been due to characteristics of the tasks (e.g., difficulty, stillness of the frames) or to capacities of the participants. It is possible that the expertise of dancers concerns a dynamic use of imagery involving complex sequences of movements and highly coordinated motor plans. It could be shown by several authors, that the expertise of movement is crucial in the movement observation and detection (e.g., Beardsworth & Buckner, 1981; Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005). However, this should not be the case for static body postures. Therefore, the line drawings of human bodies we used for the MBRT could have been just too static for any effect of the dancers' expertise to unfold. This is further supported by verbal reports from almost all the dancers after the experiment. They described their use of mental imagery in a more dynamic context. Furthermore, some dancers indicated that they are able to vividly imagine a pirouette or a battement, but not any other types of movements that are not specific to their field of expertise. Several studies have shown that the effects of expertise acquired in dance or related sports activities do not transfer to other types of movements (Weiss & Shanteau, 2003). Moreover, the relative

contribution of vision or proprioception in sport experts and dancers is not yet clear and seems to depend strongly on the actual task (Crémieux & Mesure, 1994; Golomer & Dupui, 1999; Golomer, Dupui, Sereni, & Monod, 1999; Hugel, Cadopi, Kohler, & Perrin, 1999). However, dancers are trained to rapidly imitate and execute a new movement. In the training trials of the experiment, the experimenter could observe that the dancers even had to inhibit their body movements. While sitting in front of the desk, they often tried to bring their upper body part in line with the body figure presented on the computer screen. Therefore, the highly specific and over-learned connection between perception and motor execution in dancers may have interfered with task performance. Furthermore, it is certainly possible that more pronounced differences between dancers and nondancers could have emerged with a more difficult task.

The results from the comparison between mental object rotation and egocentric body transformation in dancers and nondancers indicate that the time necessary to perform a mental body rotation or a mental object rotation may not only depend on the angle of stimulus presentation. Even though exactly the same rotation conditions were applied to both tasks, two completely different response patterns were evident. It is unlikely that the stimulus per se is responsible for this difference because both stimuli evoked an increase in RTs with increasing rotation angle in plane without depth rotation. However, when the stimuli were also rotated in depth, the response patterns differed and thus may reflect different strategies. The strategy participants use when they are facing the body figures is still not clear. However, since the RTs do not vary with the angle of stimulus presentation it seems rather unlikely that mental rotation is the mechanism participants use. Interestingly, task difficulty reversed when the stimuli were

inverted and body figures presented in front view were easier. These findings suggest that participants use different strategies depending on the perceived orientation of the stimulus. This tendency seems to be stronger for egocentric body transformation than for the mental object rotation task. Finally, dancers' training and expertise in motor imagery did not seem to improve performance in any of these tasks. However, the absence of any difference in performance does not necessarily rule out a difference in strategy between dancers and nondancers. Neuroimaging studies are necessary to further investigate potential differences between dancers and nondancers.

Summary

Based on the findings from the previous section (Experiment 1), professional dancers were tested as experts in the mental object rotation task (MORT, solid cubes used by Shepard & Metzler, 1971) and the mental body transformation task (MBRT, line drawings of human bodies similar to those used by Parsons, 1987a). Differences between experts in movement and body observation were hypothesised to verify whether the visual stimulus or whether the rotational axis is sensitive to the motor and body experience of dancers. A difference between dancers and nondancers would give further support that the two tasks, MORT and MBRT rely on dissociable mechanisms. The same tasks as in the previous section (Experiment 1) were used. The responses of dancers were corresponding to the normal participants-group, with the exception that dancers showed higher mental rotation costs in the MORT.

As seen in Experiment 1, also dancers showed an increase in reaction times in the mental rotation of objects and the egocentric body transformation

with increasing angular disparity when no rotation in depth was necessary. However, in both tasks, dancers needed more time to respond. It may be that dancers did not show any benefit in the egocentric body transformation task, because we are all experts in seeing bodies. Pictures of a real body in different postures and abstract drawings representing different body postures were used in a paired matching sample experiment (Experiment 3) in the following section in order to investigate the effect familiarity has on the body representation.

Experiment 3: Mental Matching of Body Postures

Introduction

Human beings have the ability to visualise the perspective of somebody else. Most studies have focused on the ability to visualise external scenes as a third party sees them and have investigated the mentalising processes necessary to infer mental states (e.g., Vogeley et al., 2001; Wimmer & Perner, 1983). However, a second element of perspective-taking is related to the body: An observer can mentally simulate the body configuration adopted by a third party. In fact, mentally thinking oneself into another body is necessary to visualise the perspective of somebody else: I can only work out what you see if I correctly represent the gaze direction given by your eye, head, and body positions.

Dance provides an interesting example for the study of body perspectives. In order to improve performance or to memorise a movement pattern, dancers often imagine themselves executing the movements that they watch another person performing. When the model's spatial orientation does not

match that of the observer, for example, if the observer has a frontal view of the model, then simulating the model's posture requires a mental perspective transformation (Zacks et al., 1999). However, the transformation can be done in several ways. Examples referred to as egocentric body transformation include mentally rotating one's own body into alignment with that of the observed person or rotating the other's body into alignment with one's own. Alternatively, instead of the body representation, one's spatial frame of reference can be mapped. The transformation processes involved in spatial frame references and rotating bodies differ.

It is important to highlight, however, that all these different forms of perspective transformation involve an element of mental rotation, similar to that classically described for external geometrical objects (Shepard & Metzler, 1971). Although the geometry used when the participants are themselves part of the spatial transformation remains unclear. Zacks and co-authors suggest dissociative neural systems for object-based and perspective based transformations (Zacks et al., 2000; Zacks, Ollinger, Sheridan, & Tversky, 2002; Zacks et al., 2003). The authors propose a multiple system framework where different types of mental transformation are implemented by anatomically distinct neural substrates. The assumption is supported by the event-related fMRI study of Zacks et al. (2003) which showed that mental transformation of bodies involves a different neural system than mental transformation of objects as it was emphasised by previous behavioural experiments: In contrast to the classical mental rotation task, no linear increase in reaction time was found for mentally transforming bodies (Parsons, 1987a; Zacks et al., 2002). A frequently reported difference between mentally transforming bodies and objects is the participants'

frame of reference. In egocentric body transformation tasks, participants have to change their frame of reference. In mental object rotation, however, the participants' frame of reference remains stable and the two objects are aligned along a particular axis. Interestingly, behavioural results have repeatedly shown evidence that the axis of the rotation alters even within a class of stimuli. This means that as the reaction time is not always monotonically and linearly increasing with increasing angular disparity, the path of mental rotation may be altered. One of these alterations is the change from incremental steps to a quick flip along the shortest path. A number of authors suggest that visual features like familiarity are responsible for this change (Ashton, McRarland, Walsh, & White, 1978; Mast, Zaehle, Long, Jola, & Lobmaier, under revision; Robertson & Palmer, 1983). This assumption is in correspondence with the data from egocentric body transformation and mental object rotation in both Experiment 1 and Experiment 2. For example, when participants have to match their perspective with an inverted front facing figure they do not mentally rotate incrementally 180º along the x-axes and 180º in depth along the z-axis as expected. It took participants clearly less long to respond for front-facing, inverted figures, and they reported having mentally flipped themselves backwards as described previously (Experiment 2). This means that participants seem to exchange or merge incremental steps when matching their perspective from the default position upright, from the back (Cooper & Shepard, 1975; Robertson, Palmer, & Gomez, 1987) to an inverted figure from the front by a quick flip. A similar decrease in reaction time was found when participants had to name familiar but inverted objects compared to when the objects were rotated by a few degrees only (Murray, 1997). Murray suggested that incremental rotational steps to align the familiar object with its canonical

orientation are replaced by a quick flip along the shortest path. However, it remains unclear whether the quick flip reflects simply a quantitative advantage for some mental rotation operations that have been over-learned because of the visual familiarity of one's own and other bodies or whether it reflects a qualitatively different, nonspatial way of manipulating body representations. In both cases the axis of rotation seems to be known by the participants before the stimuli are rotated or flipped onto the canonical axis. Bodies as well as familiar objects are a special set of stimuli as they possess an inherent axis that is canonically aligned with respect to the environment in a way that abstract objects need not be. The canonical axis of the observer's own body may therefore play a role in tasks which require spatial transformation between an observer and a model, or between two model stimuli (e.g., Corcoran, 1977).

In the present study, a symbolic, abstract notation of body postures was used in order to investigate the role of both the inherent axis of a stimulus and its familiarity in mental rotation. The term 'abstract' is used to emphasise that the body represented in the Labanotation is not pictorially isomorphic to a real body. As the surface form of the body represented in the Labanotation does not resemble a real body, the quick flip effect and the use of a canonical axis can be investigated even when the surface form in the presentation does not explicitly suggest them. This will give further insight into the rotational operations carried out in egocentric body transformation.

The Labanotation (Hutchinson, 1977; Laban, 1928) was developed to describe complex human movements in three-dimensional space. Visual cues that spatially correspond with a real human body were eliminated and replaced with an abstract score. Limb positions are shown on a staff rather than their true

spatial locations, and all postures are shown as if viewed from the back. An example of a posture's orientations is illustrated in Figure 7 (p.77). The egocentric perspective has to be inferred from the abstract drawings and is thus implicit rather than explicit. The information about particular body movements is transformed into the egocentric perspective of the reader's body. That is, the Labanotation represents body postures from the back, using an 'in-the-body' perspective, despite the absence of any visuo-spatial features corresponding to the normal view of one's own body. The question was therefore, whether the body transformation tasks would show a quick flip effect, with disproportionately good performance in transforming between front and back perspectives, even when the visual surface form does not naturally suggest any particular spatial transformation. An affirmative result would suggest that (1) body representations evoke an inherent, canonical axis, even when this is not apparent in their surface form, and (2) body representations support a 'flip' or 'transposition' type of transformation, distinct from mental rotation, even when this is not favoured by their surface form. Such conclusions would suggest a specific cognitive function for relating one's own body to the bodies of others, with important implications for social cognition.

Method

Participants

Twelve volunteers with a mean age of 28.9 ± 11.7 years, 9 female, all right-handed, participated in the study after giving their informed consent approved by local ethical committee. Nine participants were dance students from the Laban Trinity College London, either at their undergraduate or postgraduate level in

dance, or students from the professional diploma course in Dance Studies. All of which had at least 2 years of classes in Labanotation. The remaining participants were experienced Labanotation readers who work either in the field of Labanotation or in the field of dance.

Stimuli

The stimuli consisted of four different body postures (i.e., two classical ballet and two novel positions) chosen on the basis of pilot data (Jola & Haggard, 2006). The postures were balanced over body parts involved in the gesture and the gestures side, alignment, and direction across the stimuli (see Figure 7, p. 77). Each posture was modified for the mismatching condition in four different ways. The postures were either: 1) outline matched (similar visual shade of the posture), 2) mirrored, 3) subjected to a small change defined by a direction and level change of one body limb only, or 4) subjected to a clear change, consisting of a new arrangement of the Labanotation symbols which resulted in a clearly different but biologically possible posture while the constituent symbols remained largely the same.

The postures were either presented as pictures of a professional female dance performer or represented in Labanotation. The pictures were taken with a digital camera and had a homogenous background. The performer was naïve with respect to the hypothesis of the study. The Labanotation drawings were written with CALABAN LT computer-aided software (http://aweb.bham.ac.uk/calaban/). All notations were verified by Jean Jarrell, a Lecturer at the Laban Trinity College.

Task

The participants were instructed to make same-different judgements about pairs of body postures presented sequentially on a laptop Computer screen. The prime picture was presented for 1500 ms. After an inter-stimulus interval with a central fixation cross for 500 ms The target was presented on the screen for a maximum of 8000 ms. The participants had to respond as quickly as possible after the target picture appeared, by pressing one of two indicated keys on a keyboard with their right or left index finger to verify whether the postures were the same or different. The pattern of response was counterbalanced across participants. Each experimental condition was defined by the relationship between the prime and the target. The design included three factors, each with two levels: *target type* (target is a picture vs. Labanotation), *perspective* (no change vs. change), and *matching* (posture is the same vs. different). The matrix of Table 4 (p. 77) illustrates the different combinations for the two factors target type (columns) and perspective (rows).

The prime was always a photographic image of a female dancer in one of four postures. The target was either an image of the dancer or a corresponding Labanotation equivalent of the posture (each in 50% of the trials). In half of the trials the prime and the target posture differed in their perspective. However, as the Labanotation has an inherent back-view perspective, pairs with Labanotation targets showed only the perspective combinations back-back and front-back. By the same token, two additional perspective combinations, front-front and back-front were only available for picture targets. Consequently, target type (picture or Labanotation) and perspective (front or back) were not orthogonal but also not predictable. Furthermore, this modification in the picture-picture match was used to test whether the participants validated the target position from their egocentric

default position (upright back posture) or whether they instead changed their frame of reference to the perspective of the prime. This gave a total of 128 trials, consisting of 4 basic body postures, 4 minor modifications of each posture (mismatch), 2 locations for the postures (each of the four postures was randomly presented as the prime or the target), 2 target formats (picture or Labanotation), and 2 perspective types (no perspective change, perspective change). For picture targets, each modification was assigned randomly to one of the two perspective types.

Procedure

The participants were tested individually in a quiet room. Before the experiment started, participants' familiarity with all the symbols used in the experiment was verified. Participants underwent a training session with five trials in order to become familiarised with the task prior to the experiment. None of the postures within the training session were used in the experiment proper. If the participants made more than one mistake in the training session, the session was repeated (up to a maximum of three times). Accuracy in error rates (ERs) and reaction times (RTs, from correct trials only) were analysed. Matching and mismatching trials were merged.

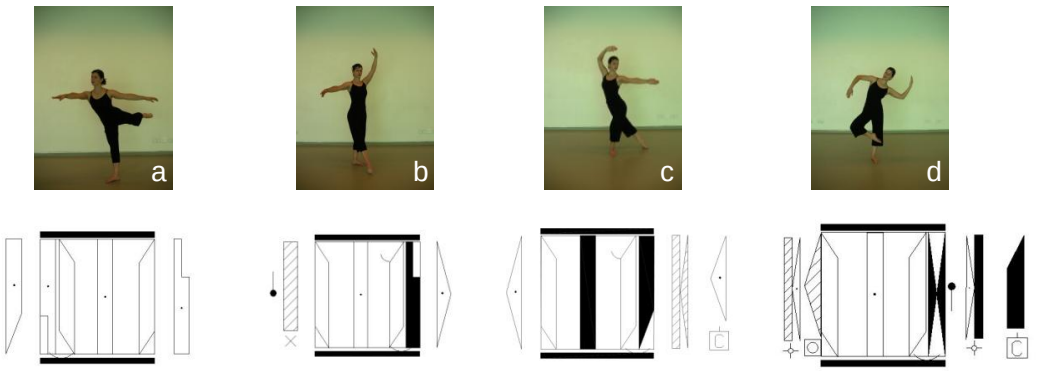
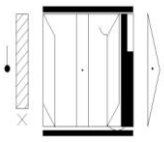
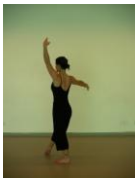
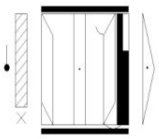


Figure 7. Body postures in pictures (upper row) and in Labanotation (lower row) used as stimuli in the picture-Labanotation matching task of Experiment 3. (a) and (b): two ballet positions with commonly aligned arms and legs, that is, arabesque and tendue, respectively; (c) and (d): two novel positions with nonstandard bent limb.

Table 4.

Conditions of Experiment 3 Illustrated with One Trial (i.e., Body Posture).

		Labanotation Target		Picture Target	
		Prime	Target	Prime	Target
Perspective Change	Front – Back				
	Back – Front				
No Perspective Change	Back – Back				
	Front – Front				

Note: As the Labanotation is always from the back, only the orientation conditions front-back and back-back are present for Labanotation targets; to ensure that participants could not foresee the target from the prime, also the orientations back-front and front-front for picture targets were included.

Results

Out of all 12 participants 3 had more than 25% ERs and were therefore excluded from the analysis. Mean RTs and mean ERs are shown in Figure 8 (p. 79). A repeated measures ANOVA with the factors target type (picture vs. Labanotation) and perspective (no change vs. change) on ERs showed significant main effects of both factors target type, $F(1, 8) = 36.90$, $p < 0.001$, and perspective, $F(1, 8) = 23.04$, $p < .01$. Furthermore, the interaction of the target type and perspective was significant, $F(1, 8) = 7.76$, $p < .05$. Paired samples *t* tests for picture targets showed that ERs were significantly higher with perspective change (14.9%) than without perspective change (4.5%; $p < .05$). In contrast, no significant difference in error rates was found between the perspective changes when the target posture was presented in Labanotation (15.6% vs. 13.5%, $p > 0.26$). That is, picture-Labanotation matches were much less affected by perspective change than picture-picture matches. This difference in ERs between picture targets and Labanotation targets is clearly visible in Figure 8 (p. 79).

The repeated measures ANOVA on RTs revealed significant main effects for both factors target type, $F(1, 8) = 88.61$, $p < .01$, and perspective, $F(1, 8) = 21.40$, $p < .05$, as well as a significant interaction between them, $F(1, 8) = 19.64$, $p < .05$. The perspective condition for both target types was compared with paired samples *t* tests separately. The analysis revealed significant differences between perspective change and no perspective change for picture pairs with increased RTs when the perspective was different between target and prime, 1.33 s versus 2.05 s, $t(8) = 9.48$, $p < .001$. No significant difference in perspective was found for Labanotation targets, 3.43 s versus

3.69 s, $t(8) = 1.74$, $p = .12$, as can be seen in Figure 8 (p. 79). The ERs for Labanotation targets were independent of perspective change in contrast to picture targets. This means that differences in RTs for Labanotation targets cannot be explained by a change in accuracy.

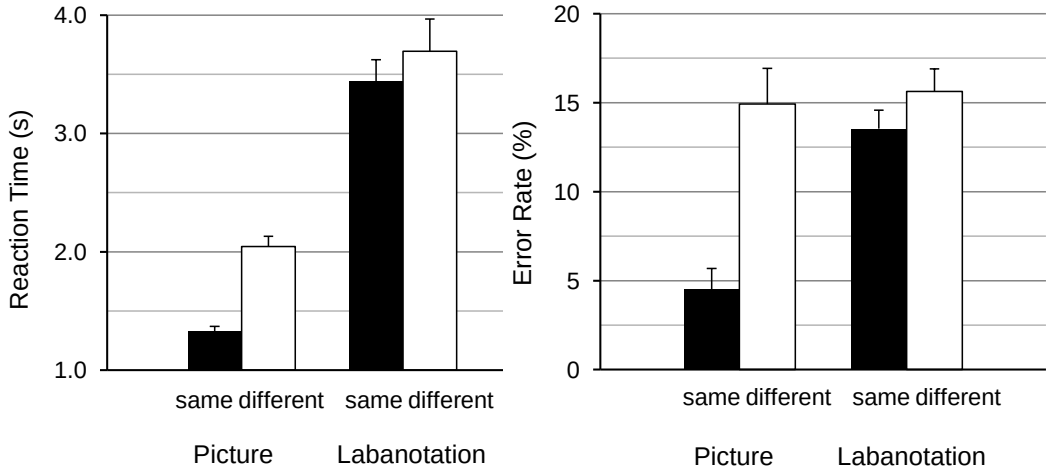


Figure 8. Mean reaction times and mean error rates (+SE) in the picture-Labanotation matching task of Experiment 3 (n = 9). X-axis: picture and Labanotation target conditions with no (i.e., same perspective, black bars) and with (i.e., different perspective, white bars) perspective change; y-axis (left figure): reaction times in seconds; y-axis (right figure): error rates in %.

Targets in the picture-Labanotation matching always presented the postures from the back while picture targets were showing postures equally often from the front and the back. In order to exclude a possible confound of target orientation repeated measures ANOVA with the factors perspective (no change vs. change) and target orientation (back vs. front) for picture-picture matching targets were computed. Corresponding to the former analysis, significant main effects were found for perspective in ERs, $F(1, 8) = 15.45$, $p < .01$, and RTs, $F(1, 8) = 73.46$, $p < .001$. However, no significant interaction of target orientation and perspective change was found. The factor target orientation showed a nonsignificant trend for longer RTs for front targets, $p > 0.07$.

Discussion

In this study, the nature of the body representation involved in egocentric body transformation was investigated in the special case where the surface form of the body representation is nonpictorial. Experiments on egocentric body transformation have generally used pictures or drawings of bodies and body limbs in different spatial relations to the participant. Reaction time and accuracy were measured in a same-different discrimination task where half of the target postures were pictures while the other half were postures written in an established but abstract notation for body postures. The pictures showed the dancer either facing the observer or seen from the back. The egocentric body transformation had to be performed solely on internally generated body representations. By the use of the Labanotation, the underlying processes in thinking oneself into the body of a third party without preventing visual familiarity could be investigated. Internally generated body representations seemed to modify egocentric body transformation when a perspective change is necessary.

The overall accuracy obtained in the matching task showed that the Labanotation was encoded to a body representation allowing posture matching. In general, encoding a Labanotation drawing makes the task more difficult. However, a perspective change in the postures only increases task difficulty when the postures are given as pictures and has no additional effect when the second posture is presented in Labanotation. Therefore, the relatively good front-back performance in picture-Labanotation pairs compared to picture-picture pairs was not due to a change in the speed-accuracy trade-off in that condition.

Picture-Labanotation matches had increased reaction time in comparison to picture-picture matches. The additional time reflects the time participants need

to read the Labanotation and transform it into an internally represented body configuration. In line with the previous Experiments 1 and 2, the expected mental rotation effect for picture targets was observed. The time to recognise body postures as pictures increased when the perspectives were different. In contrast, no such mental rotation effect was observed when the body was represented by the abstract Labanotation symbols.

The lack of mental rotation costs with Labanotation is consistent with previous reports of a quick flip onto a canonical or inherent axis. The quick flip onto a canonical axis avoids slow incremental transformation by successive stages characteristic of mental rotation (Shepard & Metzler, 1971). In previous work, the quick flip has been linked to familiarity with the stimulus and with the existence of a viewpoint-independent or object-centred mental representation of the stimulus object with its own intrinsic canonical axes (Murray, 1997). These results suggest that the human body is internally represented as such. Even when the surface form is not body-like, the data suggests that an internal body representation is generated. Moreover, it seems that the basic perspective, or inherent axis of this body representation, is an 'in-the-body' or egocentric perspective, in which observed or visualised body postures are simulated on the body of the observer. This result could also be interpreted as an effect of expertise, because Labanotation readers are used to the in-the-body, back-view of Labanotation. Learning Labanotation therefore involves learning to flip the perspective when comparing a Labanotation score with a dancer facing them. To use an analogy, deaf American signers do not show mental rotation costs for linguistic signs (Emmorey et al., 1998). The authors suggested that habitual use of the American Sign Language did increase their mental rotation skills. However,

in an additional experiment, which is not cited in this thesis, Labanotation readers compared to nonreaders did not differ in picture posture matching. The expertise from Labanotation flip therefore seems nontransferable to mental transformation of analogue body pictures. The symbolic representation of the body enables a different way of dealing with human body forms which is nonanalogue.

Could the lack of a mental rotation effect in the Labanotation matching be explained by a higher cognitive load for Labanotation targets? On the one hand the increased reaction times and error rates for picture-Labanotation matches suggest that it could. On the other hand, it can be assumed that the effect must arise from a qualitatively different coding mechanism for Labantotation and not merely from a quantitative difference in the complexity of the code itself. In particular, several studies of mental rotation showed that the more the complex the stimuli, the *steeper* the linear increase in reaction time with angular rotation (Bauer & Jolicoeur, 1996; Folk & Luce, 1987; Shepard & Metzler, 1971) or at least *not flatter* (Cooper & Shepard, 1975).

Furthermore, the results did not suggest that the only symbols were processed by categorical exclusion, which meant that postures were identified as different on the basis of one single symbol mismatch (Ashton et al., 1978). Such a facilitation strategy cannot explain the difference between Labanotation and picture reaction times. The results also reflected parallelism of cognitive processes (Sternberg, 1969). For example, the transformation between pictures and the back-view of Labanotation could have occurred in parallel to reading the details of the Labanotation itself. Picture-Labanotation matching might then indeed involve a mental rotation process, but this would be hidden in the longer overall reaction time. That is, presentation of a Labanotation target could trigger

two parallel processes, namely simultaneous encoding of Labanotation and mental rotation of the picture to an 'in the body' perspective. However, both Labanotation reading and mental rotation are, especially for reading beginners measured in this study, demanding processes on their own. Therefore, it is unlikely that they were done in parallel. In the reading classes, beginners prefer to carry a sheet of paper with the score when they have to transform the notation into movement, as looking at the score screened from the classroom projector would ask for additional mental rotation processes.

So far, the results from this experiment indicate that mental transformations based on abstract notation of body configuration stimuli are perspective independent. Moreover, performance in matching picture-picture pairs can give additional information about body representation. Corresponding orientation between prime and target was easier for both picture target orientations (i.e., front-front and back-back). Therefore, one can assume that the pictures were matched in terms of their visual surface form. However, the data showed a trend towards a main effect for shorter reaction times when the target pictures were back facing compared to front facing, independent of prime orientation. This is in line with recent findings on body and body limb perception, which assumed the observers' default internal body representation is upright from the back and this orientation should therefore be treated separately from other orientations (Ashton et al., 1978; Cooper & Shepard, 1975; Jola & Haggard, 2005; Mast et al., 2006; Parsons, 1987a, 1987b, Robertson et al., 1987; Shelton & McNamara, 2001; Wraga et al., 2003). Robertson et al. were unable to disentangle rotation of the internal body representation from changes in the egocentric frame of reference for front facing stimuli. Therefore, whether the

participants positioned themselves mentally into the figure (i.e., self rotation, change of the reference frame) or rotated the figure like an object into their spatial reference frame (i.e., egocentric rotation, stable egocentric default reference frame) remained unclear. These data indicated a trend to transform the prime to the participants' default position.

Evidence for an internal body representation which has a perspective-independent frame of reference was found. In general, tasks are more demanding when mental rotation is required (Shepard & Cooper, 1982). No increase in difficulty for posture matching with perspective change when the target posture was presented in Labanotation could be observed. The egocentric frame of reference was transformed without the processing difficulties associated with perspective change when abstract symbols were representing the body. It clearly matters whether the internal posture representation is generated from spatially equivalent or nonequivalent configurations of the human body. It seems that how the reference frames are transformed in mental object and mental body rotation is mainly determined by the type of stimulus. Pictured human bodies seem to have an inherent perspective and automatically evoke a particular relationship with the observer's own body. Similar characteristics can be assumed for familiar objects when they have a canonical view. Several studies found evidence for similar properties in mental rotation (e.g., Parsons, 1995; for an overview see Wraga, Creem, & Proffitt, 2000).

It was hypothesised that mental rotation costs would occur when the two postures in the same-discrimination task differed in their perspective. These mental rotation costs were caused either by a transformation of the egocentric perspective or by a transformation of the presented body. A lack of mental

rotation cost would indicate a quick flip which could be either qualitatively different from mental rotation or a special accelerated version of mental rotation. Abstract, nonspatial body representations showed a gradual mental rotation pattern or a quick flip pattern like those found for transformation of familiar objects and body figures. The results showed that body representations generated from body figures are perspective dependent, while internally generated body representations generated without bodily-corresponding figures are perspective independent.

In general, these results supported the hypothesis, that the human body can be represented and transformed using a symbol notation which refers to the human body. This symbolic body representation contrasts with the spatial analogue representation of the body given by vision. The canonical axis used for body representation appears to involve an egocentric perspective, or back view. In particular, processing symbolic representations involved accelerated or 'quick flip' transformation even though this axis is not explicitly represented in the notation itself. In contrast, matching of body pictures involved mental rotation of surface forms and did only reference to the perspective of the participants' own body when the matching postures are facing in a different direction.

Summary

Mental transformation of visual stimuli has been widely studied. For familiar stimuli such as human bodies, a quick flip or mental realignment to a canonical upright orientation along the shortest path has been assumed. However, it remains unclear whether and how such special, accelerated transformations depend on familiarity with the stimulus and its orientation.

In the present study, an established notation system for the human body, the Labanotation, was used to investigate spatial transformation of visually presented body forms. The alignment of the symbols on the notation staff is spatially incongruent with a human body, but always relates to a body from the back, as if in first-person perspective. Participants with experience in reading Labanotation had to match body postures in a same-different discrimination task. The postures were presented either as photos of dance postures from a variety of viewing angles or as Labanotation drawings. Comparisons of pairs of photos showed the familiar mental rotation effect, with the time to respond being dependent on the angular discrepancy in perspective between the first and second photos. However, presenting first a photo and then a Labanotation drawing produced no increase in reaction time with increasing angular discrepancy between the two represented body stimuli. Readers of Labanotation achieved a 'quick flip' between a posture represented in an explicit perspective on a photo and the egocentric perspective used for the notation. Thus, the abstract nonspatial representation of Labanotation enabled a quick flip of the reference frame. The combination of a spatial matching task and a learned symbolic code for body postures suggests that processing of human forms need not rely on analogue, embodied representations as reported previously.

Therefore, the form of the mental representation or their transformation processes is dependent of the visual presentation whilst the relation of the egocentric perspective to the canonical axis orientation of the external stimuli plays an important role. In the following chapter, experiments that investigated mental representation of the egocentric space are reported.

Chapter Three

Body Representation based on Somatosensory Information

Experiment 4: Body References in Proprioceptive Perception

Introduction

Proprioception means perception of oneself. It is the sense which provides us with sensory information of ourselves from the inside. Physiologists have studied proprioceptive sensors for several decades. In the current neurophysiological literature, the term 'proprioception' is used to refer to the set of sensory signals that originate peripherally in the body and which inform the brain about the positions and movements of parts of the body in space: the kinesthetic sense (Proske, 2005). These signals are thought to derive from muscle spindles, joint receptors, tendon organs, and skin receptors. The most studied of these, and perhaps the most important ones, are the muscle spindle afferents.

The afferent signals from sensors such as muscle spindles are fairly well understood, although their use in motor control, particularly their contribution to the sense of position, has been heavily debated (Matthews, 1977). When a muscle is stretched, the spindle afferents signal the change in its length and the velocity of that change. Although we do not often consciously attend to these signals, the evidence that muscle spindles play a partial role in the experience of

position sense is at least twofold (see Goodwin, McCloskey, & Matthews, 1972b): First, the activation of afferent muscle signals triggers an illusory perception of movement. Second, position sense persists when joints are paralysed, whereas peripherally deafferented patients who lack muscle spindle afferents are wholly reliant on vision for postural and limb motor control. Therefore, muscle spindles and joint receptors are involved in the positional sensing of body limbs, and other sensory systems such as vision can contribute. For a powerful model on body representation it is essential to understand the functional integration processes of multisensory signals.

The aforementioned studies have generally focused only on local proprioception. For example, tendon vibration studies have typically measured illusory flexion or extension by stimulating muscles spindles (Goodwin, McCloskey, & Matthews, 1972a). Microneurographic studies have recorded afferent signals from individual nerve fibres in humans (Vallbo, Olausson, Wessberg, & Kakuda, 1995) in order to identify how these signals vary with displacement of individual body parts. Nevertheless, we sense a coherent representation of the surface of our body as a whole. Therefore, it is important to understand how the sensory signals arising from different parts of the body are combined in order to construct this integrated representation of the whole body. That is, local information about the length of each muscle or the angle of each joint can be combined to represent the configuration of an entire limb, or indeed the whole body. However, we experience on a daily basis where our body parts are in space, but not the actual lengths of individual muscles. For example, a person who reaches under the table to tie their shoelace without looking at it,

clearly uses a representation of the position of the foot and of the hand, and is moreover able to relate them in an appropriate way.

The term ‘body schema’ has often been used to refer to abstract postural representation of the configuration of the body in space (Head & Holmes, 1911; Paillard, 1991). However, relatively little is known about how the brain combines multiple local signals from each point in the kinematic chain in order to produce an overall body representation. Only a few experimental studies have systematically investigated how different types of proprioceptive information from one or more body parts are combined. In tactile perception though, Martinez (1971) found evidence for a body-centred postural frame for bilaterally symmetrical movements. It is notable, that after surgical disconnection of colossal fibres, participants are not able to match the positions of one hand with the other (McCloskey, 1973). Thus, the colossal fibres provide a cross-referencing of different limbs in order to gain a positional sense of the whole body. Interestingly, Vallbo and al-Falahe (1990) found that pronounced differences in muscle spindle firing were not necessarily present during visually or proprioceptively guided movements. Therefore, afferent signals such as from the muscle spindles are not the pure basis for performance differences; cognitive representational processes play a particular role in the position sense too.

However, the representation of the body is dependent on sensory inputs. Several studies have created conflicts in the integration of different body parts into a whole body representation by manipulating sensory inputs. In these cases the brain appears to impose coherence. For example, when participants hold the tip of their nose whilst experiencing an illusory extension of the elbow induced by tendon vibration, they feel as if their nose is elongated (Lackner, 1988). This

suggests that participants maintain an internal body image which includes information about body part size. Nevertheless, it also shows that the imposition of coherence breaks down, as the nose is experienced as abnormally sized. Other examples producing physically-impossible percepts using tendon vibration include hyperextension of the forearm (Craske, 1977) or physically-impossible configurations of the whole body (Lackner & Taublieb, 1984). Thus, the position sense of the body and the body schema is calibrated over time and is actually provided by the relation of body limbs to each other, particularly when they are in spatial contact (Lackner, 1988; Lackner & Taublieb, 1983).

In many cases, the brain appears to maintain separate representations of individual body parts. For example, it has been found that wearing displacing prisms independently adapts the proprioceptive representation of the arm used during the adaptation phase, under the constriction that the head and trunk remained fixed (Hamilton, 1964; Harris, 1963; Prablanc, Tzavaras, & Jeannerod, 1975). Though the mechanisms of visual and proprioceptive integration during prism displacement are still unclear (Rossetti, Desmurget, & Prablanc, 1995), it seems that vision recalibrates proprioception of the two limbs independently either when the arm is continuously displayed during prism adaptation or when the head is immobilised. To summarise, a continuum of bodily integration seems to exist, with some aspects of body representation being purely local, while others display strong interaction and coherence of information throughout the body representation.

Position matching is an established method for investigating the spatial representation of the body (von Hofsten & Rosblad, 1988; Wann et al., 2001). In the version used here, participants indicated the perceived position of their target

hand at a range of locations (target locations) on a horizontal surface, by reaching with their other hand to the matching location on the underside of the surface. Interest in previous studies has focused on different sources of sensory information about target locations. For example, pointing errors are generally bigger when only proprioceptive information about the target location is provided, compared to when the same target location is defined purely by vision. A small but significant further improvement is found when both visual and proprioceptive information about the target location were available. This suggests that a multisensory combination of visual and proprioceptive information provides a better representation of the position of the hand in space than either sense alone (Haggard et al., 2000; van Beers, Wolpert, & Haggard, 2002). Since the reaching movement made by the hand beneath the work surface to match the target is the same in all conditions, these differences are attributed to the sensory information about the target location that is available in each condition, as opposed to the motor control of the matching hand.

Here, the nature of proprioceptive representations of hand position and the way in which they are combined with visual information was investigated in more detail. To do this, the matching accuracy of skilled dancers, who are proprioceptive experts, was compared with nondancer controls. Dancers showed outstanding performance when matching the positions of single elbow or shoulder joints in the study by Ramsay and Riddoch (2001) and also in passive knee-joint matching as investigated by Lephart, Giraldo, Borsa, and Fu (1996). In contrast, Barrack et al. (1984) found that nondancer controls were more accurate in knee-position matching. However, no study was found that investigated which aspects of proprioception are superior in dancers. This expert group was chosen

particularly to investigate whether they were better able than normal to combine proprioceptive information from several joints and muscles to generate a superior representation of the overall configuration of the body as a whole. An affirmative answer would suggest that the mind can form superordinate levels of proprioceptive body representation, presumably as a result of training, and that it would reveal the dimensions of its spatial organisation. Here, the focus was particularly on whether each limb is represented in its own independent proprioceptive frame of reference or whether both limbs are integrated to provide a common 'propriocentre' analogous to a hypothesised egocentre in space perception (Gibson, 1979). The focus was also on the relative importance of proprioception and of vision in the representation of hand position.

Method

Participants

Thirteen expert dancers and 14 nonexperts volunteered to participate in the experiment, which was approved by the ethics committee of University College London. Each participant received standardised information regarding details of the experimental procedure and gave their written informed consent prior to the testing. The expert group had an average age of exactly 19 years and contained 2 males. All experts were right handed professional dancers or dance students at a graduate or undergraduate level recruited from dance colleges and Universities in London, such as the London Contemporary Dance School and the Laban Trinity College. The control group had an average age of 21.79 years ± 0.05 months and contained 3 males, 2 of which were left-handed. All participants were

University students with no experience in dance or performance training, and all were naïve with respect to the hypothesis of the study.

Apparatus, Stimuli, and Procedure

A Perspex table (820 x 620 x 5 mm) was mounted upon three tripod stands (Hama Tripod Star 42) at a height of 120 cm. On top of the table was a black sheet indicating the target locations. A digital photograph of each matching attempt was taken using a Logitech camera positioned centrally underneath the table and fixed on the floor upon a small tripod. The target locations were marked with white sensible circular stickers (7 mm diameter). These were aligned on the left-right axis in the middle of the black sheet, with a centre-centre distance of 11.1 cm (see Figure 9, p. 94).

The participants were seated comfortably in front of the Perspex table. Their sternum was aligned with the central marker. For each participant, a spirit level was used to adjust the Perspex table and the camera lens horizontally. Before each condition, a photographic image was taken to calibrate the position of the table by lining up the centre of the image with position 410 x 310 mm on the Perspex sheet (marked with a 7 mm diameter white circular sticker).

A black circular sticker (7 mm diameter) was then placed centrally on the nail of each of the participants' index fingers. On instruction to match a specific target, the participants placed the index finger of their matching hand on the underside of the table. The participants' vision was occluded in the condition without visual feedback using a black blindfold. The blindfold was kept in place by means of elastics. For each trial, a digital image was taken of the matching hand underneath the table in order to calculate matching error. The participant was asked to return both hands to their lap in between each repetition.

Task and Design

The experiment was a target location matching experiment with a between-subjects design (dancers vs. nondancers). The task was to match one of five target locations on top of the table as accurately as possible by placing the index finger of the matching hand at the estimated corresponding location underneath the table. The information provided from above the table, the target hand, was dependent on the sensory condition, whilst the matching movement remained the same in all three conditions as illustrated in Figure 9 (p. 94).

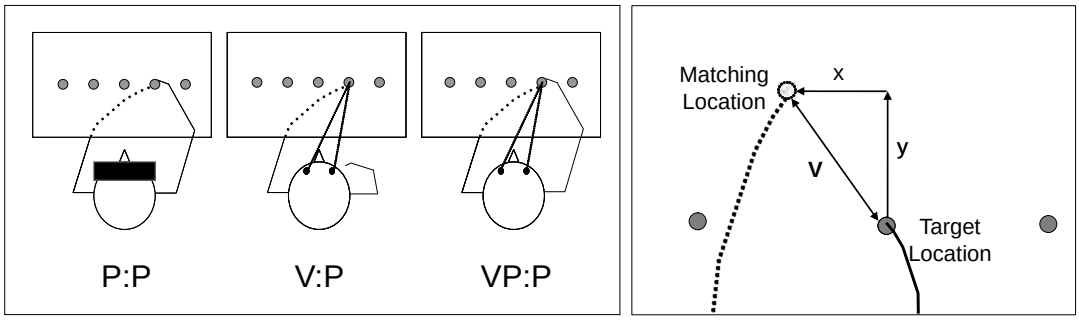


*Figure 9. The target matching task and mismatching measures of Experiment 4. Left side: illustration of the three experimental setups for the sensory conditions P:P (only proprioceptive information about the target location available from the target hand; participants blindfolded), V:P (only visual information about target location available; target hand rested in the lap position), and VP:P (multisensory condition with the target hand on the target location, which was visible to participants); right side: example of a matching attempt and the bias measures **V** (Vector), x (x-bias), and y (y-bias). The matching error is the Vector computed from mean of the x- and y-biases, the constant errors.*

In the proprioceptive condition (P:P), participants were blindfolded and the index finger of their target hand was put on one of the target locations above the table by the experimenter and then released. The participant kept their target hand on the target location and tried to match it from underneath with the other hand, thus receiving only proprioceptive feedback. In the multisensory condition (VP:P) the participants had visual and proprioceptive information about the target location.

The experimenter named the number of the target location to be matched. The participant then had to place and keep their index finger on the visible target on top of the table while attempting to match this target location from underneath with the index finger of the other hand. The task in the visual condition (V:P) was the same except that the participant kept the target hand still on their lap, thus providing only visual information about the target location.

Before and after each trial, the participant had both hands relaxed on their lap. Each of the 5 target locations was repeated 6 times in a randomised order with the right or left matching hand in each of the 3 sensory conditions. Sensory condition and the matching hand used were counterbalanced blockwise across participants. Each participant therefore performed a total of 180 trials.

Analysis

The pixel coordinates of the participants matching attempts were extracted from each picture with the Java image processing program ImageJ (Version 1.34, http://rsb.info.nih.gov/ij/) on Windows. The coordinates of the target locations were assessed for each condition and each participant separately. The matching errors were then computed by the differences between the matching and target locations, converted from pixels into centimetres. The error variables vector, regression slopes, and constant x- and y-errors were analysed in SPSS (Version 12). A subset of the data (480 trials in total) was independently rated by a second rater, and the inter-rater reliability was highly significant ($p < .001$) with a correlation of 0.8 (Pearson's r) in the X dimension and 0.9 in the Y dimension between the two raters measurements.

To access a general matching bias independent of the direction, the sensory condition was analysed by the vector bias of the matching error. For

analysis of hand bias, the constant errors of the x- and y-axis were analysed independently to allow the extent of the cross-over effect to be investigated. As a clear prediction about the factor group was present, with the dancers predicted to show a smaller matching bias, one-tailed *t* tests were used throughout.

Results

Of the 27 participants, 3 participants had to be excluded from the analysis. One expert constantly changed their hand posture and 2 control participants pointed to locations in the far right or left target locations beyond the range of the photograph in more than 80% of the trials in one condition. Consequently, 12 participants remained in each group. In 7 of these cases, the participants' nails were just off the captured picture in fewer than 20% of the trials within a condition. For these trials the pointing locations were inferred from the finger shape of the captured images.

Gender and handedness were equally matched between groups, but a nonparametric H-test showed that the dancers were significantly younger than the controls, $\chi^2(1, N = 24) = 13.87$, $p \leq .001$ (Kruskal-Wallis). Several studies have shown that proprioception improves with age (Goble, Lewis, Hurvitz, & Brown, 2005). As the hypothesis was that dancers would be more accurate, a higher average age of the control participants decreased the probability of false acceptance in this study.

Overall Accuracy

The accuracy of the target position matching in the three sensory conditions P:P, V:P, and VP:P was compared between dancers and nondancers by measuring

the vector bias of the matching error. The vector bias is the magnitude of the vector (**V**) given by the bias on the x- and y-axis in each matching attempt computed from the Pythagorean Theorem, $(x_{bias}^2 + y_{bias}^2)^{½} = \mathbf{V}_{bias}$. The magnitude of the vector bias indicates how far the participants were mismatching the target independent of the direction of the error. It therefore provides a measure of overall accuracy. The mean vector biases for group and sensory condition are shown in Figure 10 (p. 98). The figure clearly shows that both groups showed smaller vector biases in the sensory conditions in which visual information about the target location was available, namely V:P and VP:P. Furthermore, the figure indicates that the matching biases were smallest in the multisensory condition VP:P and that the matching vector bias increased when only proprioceptive information about the target location was available. In this latter condition however, the bias was smaller for dancers than nondancers whereas in the case of multisensory information dancers seemed to match less accurately than nondancers.

The univariate two-way ANOVA with the factors group (dancers vs. controls) and sensory condition (P:P vs. V:P vs. VP:P) showed a significant main effect for sensory condition, $F(2, 44) = 2.87$, $p < .04$. There was also a significant interaction between the two factors group and sensory condition, $F(2, 44) = 47.57$, $p < .001$. Independent samples *t* tests showed that dancers were significantly more accurate than controls in the P:P condition, $t(22) = 1.73$, $p < .05$, whereas the bias in the other two sensory conditions did not differ significantly between the two groups.

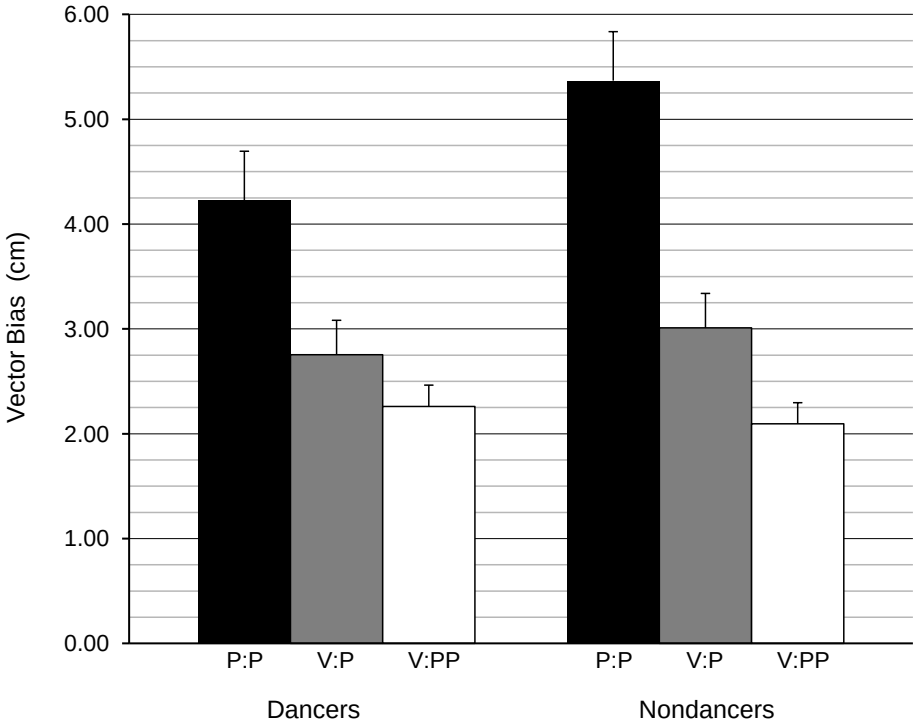


Figure 10. Mean target location matching error (+SE) for dancers and nondancers of Experiment 4 (n = 12 in each group). X-axis: sensory conditions P:P (only proprioceptive information available from the hand at the target location), V:P (only visual information available from the target location), and VP:P (visual and proprioceptive information available from the target location) for dancers on the left and for nondancers on the right side; y-axis: Vector bias in centimetres indicates participants' constant matching error.

Biases in Proprioceptive Representation

The mean constant errors in the x- and y-directions were also analysed as directional error to provide some information about the spatial reference frames used. The results are shown in Figure 11 (p. 101). Note that, in this figure, data were coded accordingly to the target hand in the P:P and VP:P conditions. In the V:P condition, there was no target hand, because the targets were purely visually perceived. Note that in order to allow direct comparison with conditions involving proprioceptive targets, the condition in which a visual target was matched by reaching with the unseen left hand is referred to as a right target.

First, systematic error patterns in Figure 11 (p. 101) can be seen in the P:P condition, with clear differences in the perceived positions between the two hands. The right target hand is perceived as being shifted to the right and rotated clockwise, whilst the left target hand is experienced with a leftward translation and a counterclockwise rotation, producing the cross-over effect reported previously (Haggard et al., 2000). However, this cross-over effect seemed less prominent in the dancers than in the controls. In the VP:P condition, misperceptions of the target hands were much less prominent and seemed to be of a comparable size for the two groups. Finally, in the V:P condition, nondancers showed a bowing in both hands, while dancers seemed to experience a similar shift as in the P:P condition, with a clear cross-over effect.

The focus was on the spatial organisation of proprioceptive representation. Translational and rotational components of the cross-over effect were analysed statistically by fitting separate linear regressions to the x- and y-values given by the six repeated trials at each target location. Furthermore, regression coefficients across hands, groups, and sensory conditions using a three-way ANOVA were compared.

The regression slopes for y-errors against target location showed significant effects of hand, $F(1, 22) = 94.70$, $p < .01$, a two-way interaction between hand and sensory condition, $F(1, 22) = 62.14$, $p < .01$, and a further three-way interaction with group, $F(2, 44) = 3.13$, $p = .05$. These analyses confirm statistically the hand-specific rotation bias for proprioceptive targets seen in Figure 11 (p. 101) and suggest that this effect differs between dancer and nondancer participants. The intercept of the y-error regression showed no main effects of group or interactions involving group and was therefore not analysed

further. The regression slope for x-errors showed no main effect of group or interactions with group and was therefore also not analysed further. However, the regression intercept for x-errors against target location showed main effects of hand, $F(1, 22) = 69.59$, $p < .01$, and condition, $F(2, 44) = 7.68$, $p < .01$, a two-way interaction between these factors, $F(2, 44) = 43.33$, $p < .01$, and a further three-way interaction with group, $F(2, 44) = 3.60$, $p = .04$. These analyses confirm statistically the translation towards the target shoulder seen in Figure 11 (p. 101).

Multisensory Fusion

In the VP:P condition, both visual and proprioceptive information about target position was available. In order to find out whether a proprioceptive reference frame was still used, the extent was tested to which the characteristic biases of proprioceptive representation were present in this fusion condition. Therefore, differences between the y-regression slopes for the left and the right hand were compared, which would capture hand-specific rotational biases in proprioception. Each participant's rotational proprioceptive bias was normalised in the VP:P condition according to their bias in the P:P condition, and their results were expressed as percentages.

Dancers showed a greater percentage of this rotational bias in the VP:P condition (37%, interquartile range expressed as IQR, 20%) than did the controls (23%, IQR 27%). These values differed significantly, Mann-Whitney U = 104, p (Z(U)) = .03. A nonparametric test was chosen for this comparison because normalisation by very small rotational biases in the case of a few participants heavily distorted the distribution of percentage values.

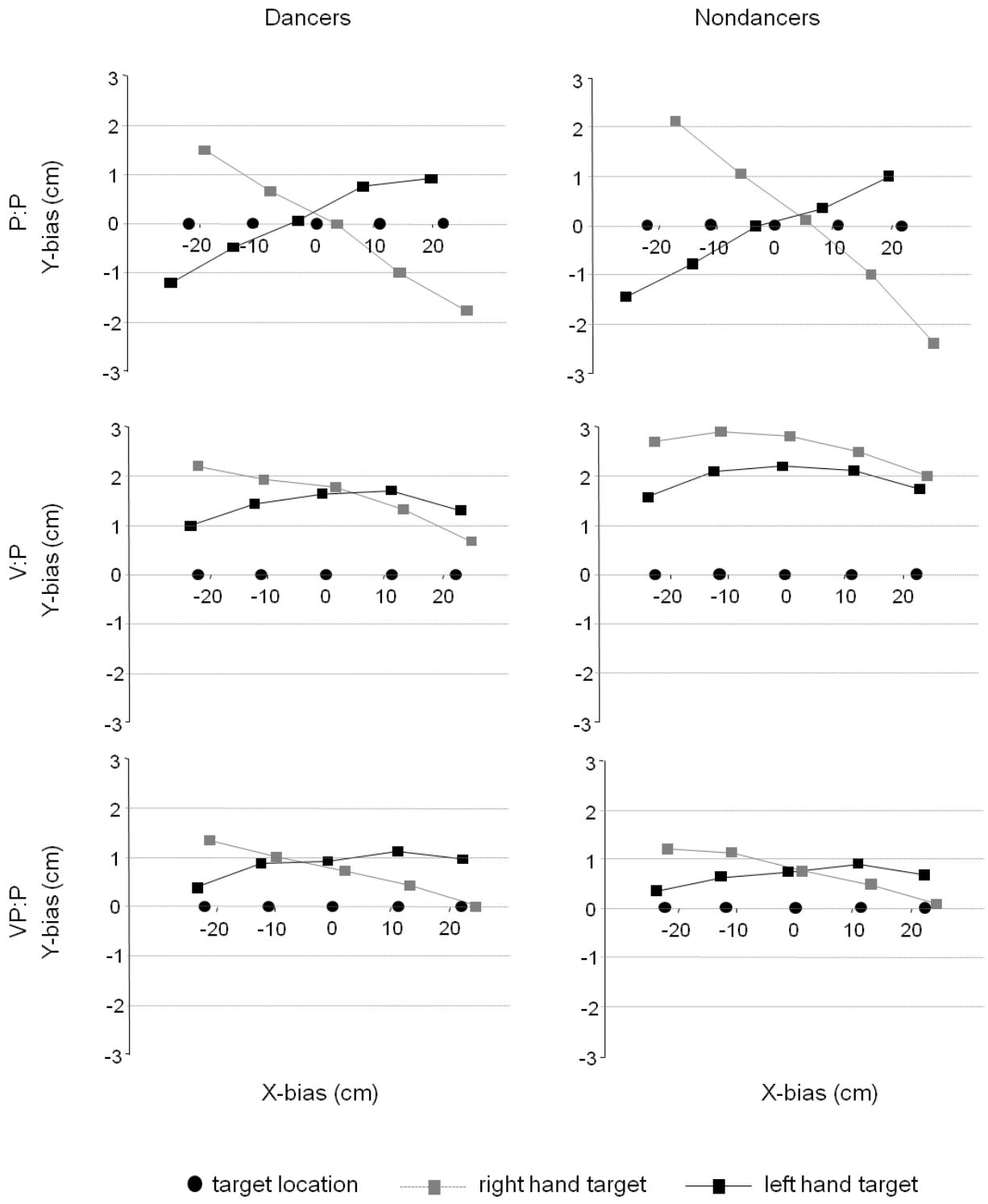


Figure 11. Dancers' and nondancers' directional errors in the target location matching task in Experiment 4 (n = 12 in each group). X-bias and y-bias in all three sensory conditions; P:P (top figure), V:P (middle figure), and VP:P (bottom figure); x-axis: target locations (black circles) and mean matching attempts (x-bias) for right (grey squares and lines) and left (black squares and lines) target hand; y-axis: y-bias for dancers (left figures) and nondancers (right figures).

This procedure was repeated for the hand-specific translational proprioceptive bias by calculating the difference between the x-regression intercepts for the two hands and normalising each participant's translational proprioceptive bias in the VP:P condition according to their bias in the P:P condition. Dancers also showed a greater percentage of the translational proprioceptive bias in the VP:P condition (46%, IQR 43%) than did controls (23%, IQR 24%). These values again differed significantly, Mann-Whitney U = 101, p (Z(U)) = 0.05. Thus, the dancers' performance in the multisensory condition suggested that they relied more on a proprioceptive frame of reference than the controls.

Further Analyses

Two further exploratory analyses were performed to follow up patterns visible in Figure 11 (p. 101). First, the figure shows that the proprioceptive rotational bias of the cross-over effect is asymmetric: The slope is more prominent for right than for left hand targets. This unpredicted result suggested a possible hand dominance effect. To capture this asymmetry the two signed regression slopes were added together and restricted the analysis to the right-handed participants. The resulting asymmetry was significantly different from zero, $t(19) = 42.5$, $p < .01$, confirming a more prominent proprioceptive bias for the dominant hand in right-handers. This advantage for the nonpreferred arm-hemisphere in the use of position-related proprioceptive information of right handed participants over the preferred arm-hemisphere has also been recently reported by Goble, Lewis, and Brown (2006). This asymmetry did not vary significantly with group or sensory condition.

Figure 11 (p. 101) illustrates a further unpredicted result. In the V:P condition, dancers showed a reduced version of the cross-over effect seen in the P:P condition. In contrast, control participants showed a pattern closer to the

perceived bowing of visual space reported previously (Wolpert, Ghahramani, & Jordan, 1994). Analysis of the y-regression slopes for the dancers' V:P data only, confirmed the residual cross-over effect in this condition, $F(1, 11) = 24.38$, $p < .01$, and also the asymmetry between right and left hands in the right-handed dancers, $t(10) = 2.47$, $p < .03$. This point is outlined in the discussion section below.

Discussion

In this 3rd chapter, effects of expertise on the mental representation of the body and its relation to the egocentric space were investigated by asking expert dancers and control participants to match the perceived position of their hand in space. The three sensory conditions used differed with regards to the sensorimotor feedback available from the target location, while the matching movement underneath the table was kept the same in all sensory conditions. Differences in matching the target position can therefore be attributed to the sensory condition of the target hand above the table and do not refer to the matching movement.

The results replicate previous findings of better than average proprioceptive representation of the upper limbs in expert dancers (Ramsay & Riddoch, 2001). More importantly, the spatial pattern of matching errors revealed the way that proprioceptive information is built up from local signals such as those originating from muscle spindles into a spatially organised representation of the body. A key finding was the constant error in proprioceptive matching which depended on the combination of target hand and target location, known as the cross-over effect from previous studies (Haggard et al., 2000). The

perceived position of the right hand at targets in the frontoparallel plane was shifted towards the right shoulder and rotated counterclockwise in the direction of shoulder extension in this study. The perceived position of the left hand at the same target locations showed opposite translational and rotational biases, thus leading to the cross-over pattern. These biases suggest that there was no single egocentre used for proprioceptive representation. Rather, each limb was represented in a frame of reference linked to its own 'propriocentre'. The present experiment revealed several new features of this propriocentric space.

First, the propriocentres for each limb are themselves supposedly linked to a superordinate representation of the body as a whole. Expert dancers showed to have less disparate propriocentres than normal control participants. Put another way, dancers represented their two arms as unified within a single, coherent body representation to a greater extent than controls. This difference could have arisen because dancers have acquired a more coherent body representation during the course of training or because individuals who have more coherent body representations are more likely to become dancers. Several studies have shown effects of training in both directions on internal body-consciousness (Adame, Radell, Johnson, & Cole, 1991; Skrinar, Bullen, Cheek, McArthur, & Vaughan, 1986; Skrinar, Williams, Bullen, McArthur, & Mihok, 1992), thus supporting the suggestion that a change in the body representation due to training is likely.

Second, the two propriocentres seemed to be asymmetrically organised, with the dominant right hand showing a more strongly biased proprioceptive frame of reference than the nondominant left hand. This latter finding suggests that the existence of separate propriocentres for each limb is not simply due to a

constant error in the perception of a particular joint angle. It does, however, reflect the functional representation of the region of peripersonal space defining each arm's normal sensorimotor action. A previous study of perceived position (Tillery, Flanders, & Soechting, 1994) posited the existence of an inter-individual 'motor fovea' for each hand, defined as an area of peripersonal space where matching errors are reliably low. The results suggest that each arm has a characteristic spatial bias pattern as well as a characteristic spatial accuracy pattern with between-subjects differences. Interestingly, a previous study has shown that the trunk serves as a reference for dancers and nondancers when participants have to position their legs at a particular angle (Mouchnino et al., 1993). The difference in the functional use of arms and legs seems to play a particular role in the formation of reference points of the human body.

Third, the results addressed the question of multisensory fusion. Previous results have suggested optimal multisensory integration with visual and tactile sensory information about object properties (Ernst & Banks, 2002) as well as with visual and proprioceptive sensory information of one's own body (van Beers et al., 2002). That is, the weighting of the multisensory integration is dependent on the reliability of each of the two signals. Here, the presence of translational and rotational proprioceptive biases was used in conditions where both visual and proprioceptive information about target position was available, as a novel way of measuring how proprioceptive information is weighted. Van Beers et al. found that vision dominated proprioception in general, but this was dependent on the spatial direction in relation to the participants egocentric shoulder position in which the matching movements were made. Furthermore, the proprioceptive signal was stronger when the target hand was actively moved by the participant

compared to when it was passively moved (Janwantanakul, Jones, Magarey, & Miles, 2002). This means the participants' matching in the VP:P condition could have been more accurate than in the P:P condition because of the stronger proprioceptive signal available. However, other studies did not find this advantage for actively moved hands in position sense (Djupsjobacka & Domkin, 2005; Lönn, Crenshaw, Djupsjöbacka, Pedersen, & Johansson, 2000). Thus, efferent information may be necessary for position sense, but it is available in both active and passive movements as shown by Gandevia, Smith, Crawford, Proske, and Taylor (2006). The estimated contribution of proprioception in the fusion condition in this experiment was 23%, consistent with other values derived using quite different procedures by Ernst and Banks. More importantly, dancers, who had more accurate proprioception than controls, weighted proprioception significantly higher in the fusion condition.

To the best of my knowledge, this was the first report of strategic inter- and intra-individual differences in multisensory position matching. However, how the uncertainty of a sensory signal was taken into account by the brain when integrating them to produce a single multisensory representation is unclear. The brain can obtain each signal's information value either by estimation from the noise in incoming sensory information or the estimation can be based on knowledge acquired through experience. It is possible that lower noise in the dancers' proprioceptive signals changed the proprioceptive weight in multisensory representation. Indeed, several studies have shown that proprioceptive accuracy develops with age (Goble et al., 2005; von Hofsten & Rosblad, 1988), thus supporting a modification by acquired proprioceptive experience.

A quite unexpected result from this experiment was the persistence of proprioceptive biases in the V:P condition in dancers but not controls. This was the case even though the participants had no proprioceptive information about target position in this condition since their target hand was resting in their lap. This seems to support the idea that experience modifies the weighting of sensory signals even if it can lead to reduced performance. Dancers might perhaps have used kinesthetic imagery in this condition, imagining their target hand was in fact on the visual target location, and then matching the resulting proprioceptive image with the matching hand. This speculation is supported by the finding that dancers displayed right-hand dominance effects in the V:P condition similar to those in the other conditions, in which a genuine proprioceptive representation of target position was allowed. It was also previously suggested by Golomer, Crémieux, Dupui, Isableu, and Ohlmann (1999) that dancers might shift the sensorimotor dominance from vision to proprioception. Therefore, only dancers may mentally simulate the proprioceptive sensation associated with visually perceived peripersonal space. It seems thus that not only can vision partly substitute proprioception in patients lacking proprioceptive information (Ghez et al., 1995; Ghez & Sainburg, 1995; Nance & Kirby, 1985; Rothwell et al., 1982; Sainburg, Ghilardi, Poizner, & Ghez, 1995), but the dancers' results pattern suggested that experts can also substitute visual information with proprioception, even in cases where the proprioceptive sense had to be mentally simulated.

Finally, the results have specific relevance to dance. The importance of proprioceptive representations in learning, attaining, and maintaining body positions has long been recognised in performers in general (Alexander, 1971; Feldenkrais, 1972) and in dance in particular (Fitt, 1988; Fortin, 1995). Several

papers have previously reported superior proprioception in expert dancers (Golomer & Dupui, 2000; Golomer, Dupui et al., 1999; Lephart et al., 1996; Mouchnino et al., 1993; Ramsay & Riddoch, 2001; Schmitt, Kuni, & Sabo, 2005; Vuillerme, Teasdale, & Nougier, 2001). Yet, the precise ways in which dancers' proprioceptive representations differ from those of nondancers have not previously been investigated. A possible improvement in proprioception by training has been questioned (Ashton-Miller, Wojtys, Huston, & Fry-Welch, 2001). In addition to being generally more accurate in proprioception, dancers showed a more coherent proprioceptive representation of their body. Their sense of hand position in space was less limb-specific and used a frame of reference closer to a common egocentre rather than to disparate propriocentres for each limb. Moreover, these factors lead dancers to weigh proprioceptive information more and visual signals less compared to controls when forming multisensory body representations. Put another way, the dancers' body schema was more intrinsic and less extrinsic than the nondancers'. There is a lively debate in the dance literature about whether the ubiquitous presence of mirrors in training environments does or does not assist in attaining and maintaining desired positions. However, it has rarely been investigated experimentally (Radell, Adame, & Cole, 2003). The results suggest that dancers are in any case less influenced by visual information about body position. Further studies might investigate whether performance on proprioceptive tests, or robustness of proprioception to visual over-ride, make good prognostic tools in dance trainees.

To conclude, these results suggest that proprioceptive information is not represented only at the local level of individual muscle lengths. Rather, local proprioceptive information is combined into at least two superordinate levels of

organisation. The 1st level of organisation involves combining local signals from individual degrees of freedom into a representation of the position of the hand in space. This level of representation is required to match one hand's position with the other. Moreover, a 2nd level of superordinate representation can be suggested, in which the propriocentres of the individual limbs are related to a common egocentre. The degree of integration of these propriocentres into a common egocentre differs between individuals, either due to sensorimotor experience or due to unidentified genetic factors. The process of integrating local somatic sensory information into a coherent representation of the whole body is an important part of bodily self-consciousness (O'Shaughnessy, 1995).

Summary

Continuous integration of multiple sensory information gives us a clear knowledge of where our limbs are in space. Recent studies have shown evidence for optimal integration of the available sensory information. The current experiment investigated whether the contributions made by proprioceptive and visual sensory information to create a whole body representation were sensitive to expertise. Dancers as experts were compared with controls in a target position matching task. When proprioceptive information from the target hand was provided, dancers and nondancers showed a rotational shift towards the shoulder of the matching hand. Thus, the data replicated previously reported hand-bias, illustrating two proprioceptive centres located at each shoulder. The dancers' hand-bias was smaller than that of the controls, but they also showed a similar effect without proprioceptive feedback. This study showed, for the first time, that

expertise leads to a more centrally integrated body representation which can be accessed by mentally simulated sensory information.

The question herein is whether the shift of the body centres affecting the perception of the egocentric space was necessary for the proprioceptive body representation. In the following Experiment 5, the sense of touch was used to investigate how space on the body surface is perceived.

Experiment 5: Body References in Tactile Perception

Introduction

The world around us can be perceived by multiple sensory systems. This study investigated how localisation of tactile experience is altered by visual and motor feedback. Touch is a specific sensory system in several respects. It is the most differentiated and important member of the somatosensory system (Schmidt, 1995) and clearly the most intimate of all senses. Also, of all sensory systems, touch is the only double sensation. By using our sense of touch, we can perceive different surfaces and shapes of objects through active touching and we can localise passive tactile sensations on our body (Gibson, 1962; Loomis & Lederman, 1984). Imagine yourself coming home late at night, for example. Even in complete darkness, you can identify a set of keys next to other objects in your pocket by actively touching them, and by scanning the door with your fingertips keyholes are found. Once inside, we are able to find our way through the interior through tactile sensation on different locations of our body, for

example when unexpectedly hitting furniture. Clearly, touch is relevant in perceiving our bodies as well as objects in the external world.

Most tactile sensations are elicited by external stimulation on the skin. The skin covers the whole of our body defining an important line between the inside and the outside, between our egocentre and the external environment. Nevertheless, the coherent sensation of the whole body, which is closely connected to the sensation of ourselves, is mainly provided by proprioception (O'Shaughnessy, 1995). Proprioception is a somatosensory system which receives information mainly from joint receptors and muscle spindles about the body position (see Experiment 4). We can, for example, hit a mosquito biting us on the appropriate location on the body without conscious effort. This means we can easily locate the point of touch on our body or name the body part where we have been touched, but to hit the mosquito we need to integrate the sensed pain with information from other sensory modalities such as vision or proprioception. Several studies have shown cross-modal effects between most sensory modalities. For example, both touch and proprioception are necessary when haptically perceiving 3-D objects. Several studies also showed a close connection of touch and vision. Vision generally improves spatial tactile resolution in humans (Kennett, Taylor-Clarke, & Haggard, 2001). However, in blind people, tactile spatial acuity is superior to sighted people, indicating cortical plasticity (Van Boven, Hamilton, Kauffman, Keenan, & Pascual-Leone, 2000) by sensory substitution. Furthermore, intermodal matching of vision and tactile sensation leads to a distortion in position sense: When a subject's hand is stroked while looking at a rubber hand being stroked congruently, the participant experiences his or her own hand at the position of the artificial rubber hand (Botvinick &

Cohen, 1998). Thus, visual and tactile-proprioceptive simultaneity are responsible for this so-called ‘rubber hand illusion’ which can be enhanced by motor activity (Tsakiris et al., 2006). The integration of different sensory modalities, such as touch, vision, and proprioception, play an important role in our everyday life. However, how the aforementioned sensory systems, vision and proprioception, connect and intervene in tactile perception of the body surface is not fully understood.

When the skin is stimulated externally, mechanoreceptors within the skin send information to the brain where the information is integrated with other sensory information in a whole body representation and then, if necessary, transferred to motor commands for appropriate action. In the somatosensory cortex, the body is somatotopically organised reflecting the tactile resolution by the size of the receptive fields. Functionally important body parts, such as the fingers, have a higher tactile resolution and are reflected by a bigger area in the somatosensory cortex. The *homunculus* is a commonly used metaphor for this cortical map of the body. It represents the surface of the human body by its cortical size. The resolution of the touch sensors on the skin can be gained by the classical two-point discrimination first investigated by Weber (1975). Contrary to the somatosensory cortex, the body is less structurally represented by its parts in the motor cortex. Thus, the body is thought to be represented by two distinctive systems; motor and perceptual. These two forms of body representation are widely discussed either as body schema dealing with the relation of perception and action or as body image bound to visual perception of the body (Paillard, 1999). Is the perception of the body by tactile sensation particularly influenced by the motor or visual bases of the representation?

The division of the body into different body parts is a stringent characteristic in body perception which is dependent on sensory feedback. Behavioural and neurological evidence accounts for the division into body parts from tactile localisation experiments and the somatotopic representation, respectively. In tactile localisation the responses were more accurate when the tactile stimuli were closer to a joint (Cholewiak & Collins, 2003). Thus, the joints act as particular reference points. However, recent studies have shown that the proprioceptive and motor body representation have several reference points (Gentilucci, Jeannerod, Tadary, & Decety, 1994; Haggard et al., 2000; Mouchnino et al., 1993) which can be shifted by physical expertise such as dance (see Experiment 4) or by actually executing a movement (de Vignemont et al., 2009). This means that there is a connection between action and tactile perception. In moving, proprioceptive feedback is provided. The bias in pointing to target locations in egocentric space thus indicated two propriocentres, one at each shoulder, instead of one at the body centre (see Experiment 4). The data of this study showed, that expertise diminishes the proprioceptive bias by a shift towards the centre of the trunk. Furthermore, unifying effects of the body parts into a whole, less segregated body were found by motor activity (Tsakiris et al., 2006). With respect to the cortical projection of the body in the somatosensory cortex, a perception of our body as divided into different body parts can at least be partially assumed for the body image, the proprioceptive perception. However, as mentioned above, the motor cortex is less somatotopically organised. Notwithstanding behavioural and neurological findings which also suggest intervention by other sensory systems, detection of a tactile stimulus is dependent on the receptive field with respect to the tactile stimulation. Sensory

signals from tactile sensations are integrated with afferent information from other sensory modalities, namely eye movement afferents (vision) or proprioceptive feedback (action), and transformed into efferent commands.

The present experiment was conducted to investigate the perception of the tactile body surface by observing localisation biases in different sensory response modes. The tactile perception was accessed on the palm and the forearm, across the wrist. If the wrist acts as a reference point in tactile perception irrespective of the visual or motor response mode, then the response pattern was expected to be the same for both response modes, thus resulting in fewer errors in all conditions the closer the participant has been touched to the wrist. In contrast, if tactile sensation is coupled with one of the other senses, namely vision and proprioception as often suggested, then differences in the response pattern were expected dependent on the response mode (proprioceptive information is pertinent in the motor response mode).

Choleviak and Collins (2003) delivered tactile stimuli at one of seven locations 25 mm apart on the forearm and asked participants to localise the stimulus on an isomorphic linear seven-button keyboard. They observed greatest accuracy near the joint. However, the use of 25 mm measure units was not precise enough. Furthermore the authors relied on the transfer of tactile localisation on a visual display, involving solely the body image. In contrast, Parrish (1897) asked participants to point to where they have been touched, appealing to the body schema. The authors found the same effect of joint attraction. In the experiment described below, these two kinds of measures were investigated in order to study the influence of joints on tactile localisation, using visual and motor response modes.

Considering the reported differences in body representation by action and perception, joints segmenting body limbs should have less of an effect in action than vision. Furthermore, vision has been found to increase accuracy of tactile location in general. Therefore, it is reasonable to assume that efferent information of the touch itself, as well as the efferent and afferent commands for action and visual perception, is decisive in perception of tactile location on the body surface. In the case vision and action do not provide equal information, a difference in multisensory integration should be observable with more accurate responses in tactile location by visual than by motor response.

Method

Participants

Eighteen healthy participants took part in the experiment which was approved by the ethics committee of University College London. Each of the participants received standardised information regarding details of the experimental procedure and gave their informed written consent prior to testing. The mean age was 28.6 ± 1.6 years. Half of the participants were females and 2 participants were left-handed. All participants were naïve with respect to the hypothesis of the study.

Materials, Design, and Procedure

Participants sat at a table, with the left forearm and the left hand comfortably extended on the lateral side hidden within a box. Neither the left forearm nor hand was visible for the participants. Tactile stimuli were delivered with the tip of a pen for approximately 1 s. The loci of stimulation were marked on the

blindfolded participants' left forearm at -40, -30, -20, -10 mm, 0 (wrist) and on the palm, +10, +20, +30, +40 mm before the experiment started (the wrist was localised at the skin fold when the participant bent the hand towards the forearm). After being touched, the participants were asked to localise the tactile stimulation presented to their left arm in two response modes, either visual or motor. For the visual response a ruler was positioned on the box directly above and parallel to the forearm. The ruler positioning was offset by a random distance on each trial to prevent participants remembering ruler values across trials. Participants had to report the ruler position where they felt they were being touched, in bird's eye view. For the motor response, participants had to point with their right index finger to the location on the box immediately above the tactile stimulus. The experimenter noted the location using the ruler. The 2 response modes were blocked and counterbalanced. Each of the 9 tactile locations was touched 5 times in a randomised order in both response modes making a total of 90 trials.

Analysis

Performance was analysed using the signed error (mean of the difference between perceived location and actual location) in order to observe the direction of the estimation error. Differences in the mean (*M*) ± standard error (*SE*) in centimetres for the location estimation in the two response modes vision and motor were tested for significance with SPSS, Version 11.5. During testing, it could be noticed that 1 male and 1 female participant touched the end of the box with their left finger tips and were therefore analysed separately.

Results

The ANOVA with the factors response mode (visual vs. motor) and stimuli location (-4/-3/ … +3/+4) showed a significant main effect for stimuli location, $F(8, 120) = 6.72$, $p < .001$. The factor response mode did not reach significance. Figure 12 (p. 118) displays the shift of the mean signed error for each stimulus location. The distance between the stimulus location (black point) and the motor or visual response is the mean signed error. As can be seen in the figure, the touch locations are perceived closer to the body centre at all stimuli locations manifested in a proximal shift. Within-subjects contrast analysis showed that this shift is significantly linear, $F(1, 15) = 12.59$, $p < .05$, with decreasing errors for more proximal locations as shown in Table 5 (p. 119). Despite a significant difference for response mode, the signed error was constantly smaller in the motor (-2.47 ± 1.00) than in the visual response mode (-3.56 ± 1.12) as can be seen in the Figure 12 (p.118). As 2 participants touched the end of the box, individual responses for each participant including those were figured out, in order to verify whether any effect of this additional tactile information can be observed. These individual responses are displayed in Figure 13 (p. 120). Lines above the dotted horizontal line at zero indicate a distal shift (positive signed error) whereas lines below are given by a proximal shift (negative signed error). A signed error of zero would lie on the dotted horizontal line across the graph.

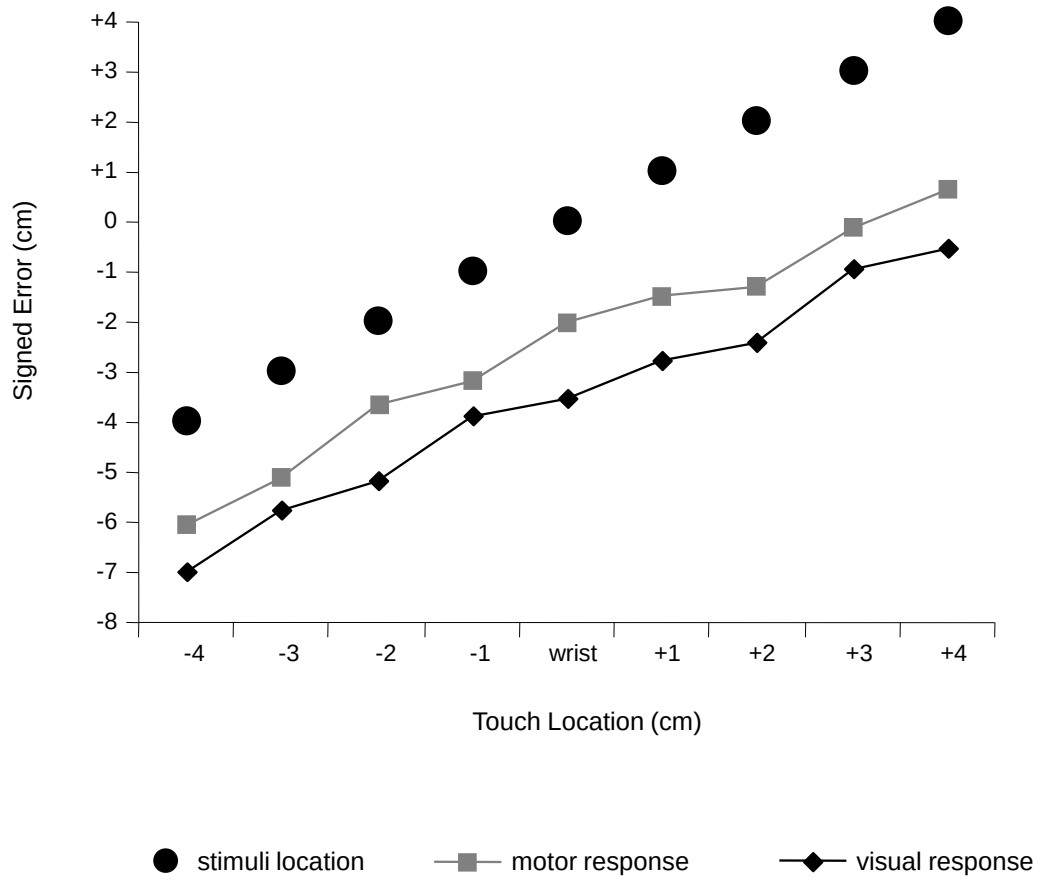


Figure 12. Accuracy in touch location estimate as mean signed error in Experiment 5 (n = 16) with actual locations of touch on the forearm (black circles), motor responses (grey line and squares), and visual responses (black line and squares). X-axis: touch locations on the forearm (minus), the wrist (wrist), and the palm (plus); y-axis: deviation from the stimuli location by the signed error in centimetres.

The two black bold lines highlight those participants who touched the end of the box during the testing. It is clearly visible that 4 participants overestimated the distance from the body to the touch at all nine stimuli locations, resulting in a distal shift. One of these is the male participant who was excluded from the analysis. This male participant was retested, as were 2 participants with a distal shift, to verify whether any faults in the testing procedure were responsible for this direction difference in the signed error. Shifts in the signed error of these 3 male participants from the test and re-test measurement (i.e., 1st and 2nd

measure), are shown Figure 14 (p. 121). The box was modified so that none of these participants could reach the end of the box in the re-test measurement. All retested participants had larger than average hands and it was evident that touching the end of the box was very likely in the primary test by these participants.

Table 5

Mean Signed Error (±SE) in Centimetres for both Response Modes (vision and pointing) of all Participants at all Target Locations on the Left Forearm of Experiment 5.

Target Location	Deviation[a]
+4	-3.936 ± .941
+3	-3.548 ± .984
+2	-3.854 ± .990
+1	-3.104 ± 1.054
wrist	-2.761 ± .967
-1	-2.517 ± .963
-2	-2.432 ± 1.108
-3	-2.423 ± 1.155
-4	-2.518 ± .997

Note: Target locations were each 1 cm apart from each other. Deviation in cm. [a]*n* = 16.

The motor response mode showed a clear distal shift. A repeated measure ANOVA with only 3 participants and the factors measurement (1st vs. 2nd) and response mode (visual vs. motor) showed a significant main effect for response mode, $F(1, 2) = 77.56$, $p < .05$, with a significant bigger signed errors in the visual (-2.2 ± 0.41) compared to the motor response mode (1.14 ± 0.26), paired *t* test, $t(2) = 8.81$, $p < .05$. The main factor measurement showed a strong trend with only 3 participants, $F(1, 2) = 12.91$, $p = .069$. The interaction did not reach significance.

As the factor measurement showed a strong trend, a paired-samples *t* test was conducted. This analysis showed significant differences between the 1st and 2nd measure in the visual response mode, $t(2) = 9.25$, $p < .05$. Furthermore, the difference between the visual and motor response mode was significant for the 2nd measure, $t(2) = 4.64$, $p < .05$, but not significant for the 1st measure, $t(2) = 2.78$, $p = .11$. In addition, a two-way repeated measures ANOVA was conducted for the factors stimuli location (-4/-3/ … +3/+4) and measurement (1st vs. 2nd). The main factor stimuli location was significant, $F(8, 16) = 3.80$, $p < .05$, with decreasing errors for more proximal locations. The signed errors of the 2nd measure showed a strong trend to be bigger (-2.94 ± 0.87) and shifted towards the body compared to the 1st measure (1.88 ± 0.54 cm), $F(1, 2) = 12.91$, $p = .07$.

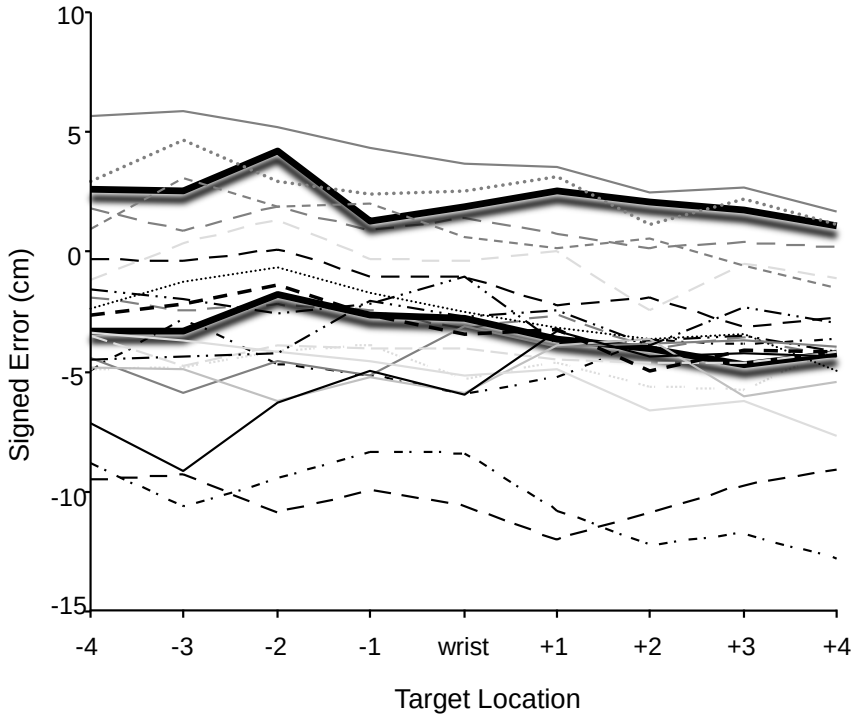


Figure 13. Individual responses in the target location matching task in Experiment 5. The distal and proximal shift of the 2 participants who touched the end of the box with their finger tips (male and female, respectively) are highlighted (shadowed black bold line); x-axis: tactile locations on the forearm (minus), the wrist, and the palm (plus); y-axis: mean signed errors in centimetres of all trials in both response modes for each single participant.

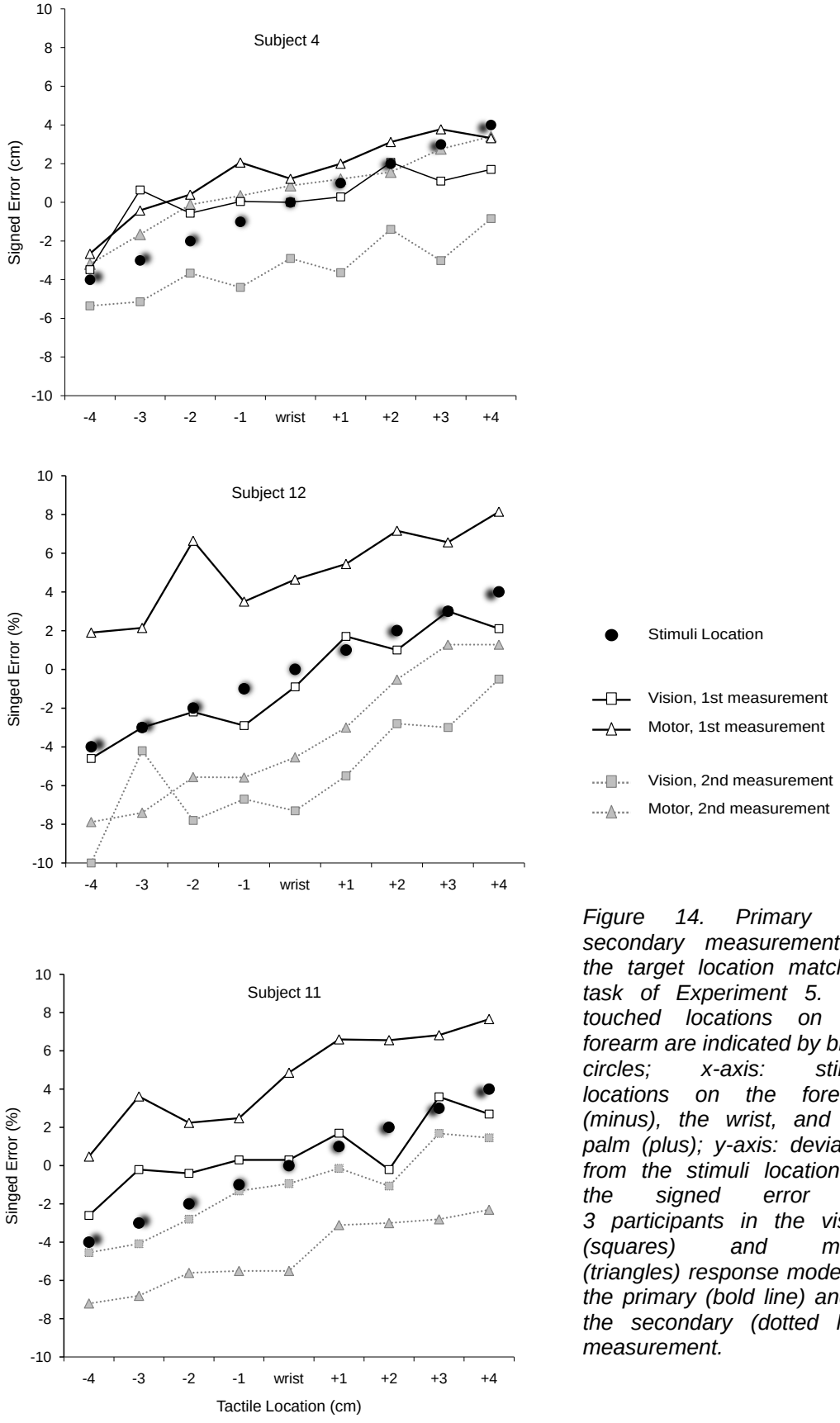


Figure 14. Primary and secondary measurement in the target location matching task of Experiment 5. The touched locations on the forearm are indicated by black circles; x-axis: stimuli locations on the forearm (minus), the wrist, and the palm (plus); y-axis: deviation from the stimuli location by the signed error for 3 participants in the visual (squares) and motor (triangles) response modes in the primary (bold line) and in the secondary (dotted line) measurement.

Discussion

How the visual and motor response modes modify tactile localisation estimation was investigated in the experiment described above. Participants were touched at nine different locations on their left arm distributed from the palm to the forearm. Thereafter, they had to estimate where they felt they had been touched either visually or by pointing with their right index finger on the box that covered their left arm. The data showed that participants in general estimated the location closer to the body than where they had actually been touched. Thus, the bias can be described as a proximal shift with a small decrease of the shift towards the body. The more the peripheral participants were touched, the greater the mislocation-span. The shift was equal for visual and motor responses. That is, the body centre acted as a reference for both visual and motor responses, although there was a strong trend for a bigger proximal bias for visual responses.

Furthermore, the data showed individual differences in the shift direction. While most participants showed a proximal bias by underestimating the distance from the body centre to the location of touch, 4 participants overestimated the body to touch distance, leading to a distal mislocation. A retest of 3 of these participants showed that it is likely that those participants touched the end of the box in the primary setting, like the 2 participants who were excluded from the analysis for which it was noticed during the 1st testing. The reversed shift was no longer present in the 2nd measurement. As 1 participant was touching the end of the box and was therefore excluded from the initial testing, the experimental setting was adjusted in the retesting in order to prevent any contact at the fingertips. All retested participants had larger than average hands. Therefore, it is likely that the touch was not noticed during the 1st measurement and that this

additional tactile information from the fingertip was responsible for the reversed shift in the distal direction. The retest confirmed a bigger effect for the visual than the motor response mode. The analysis of the data from the 2nd measure revealed a significant difference between the visual and motor response. Interestingly, the errors were significantly different for the nine target locations. Again, the bias was smaller for the locations closer to the body than the more peripheral locations. Even though only 3 participants were retested, significant main effects in the response mode as well as in the target location were evident between the 1st and 2nd measurement. However, it has to be mentioned that α error corrections were ignored. Further experiments investigating the sensory integration of touch sensation and visuo-motor senses should be conducted, factoring in additional tactile information in the experimental design. For example, it remains unclear whether the additional tactile information was relevant due to a change in reference points, due to an increase in tactile sensation, or simply due to the information where the arm ends.

The results are threefold. Firstly, the mislocation reflects that touches are generally experienced closer to the body than where actually applied. This is supported by the finding that the proximal bias was insensitive to the response mode. Secondly, when the participants were touched further away from the body centre, the shift towards the body was bigger and vice versa. This is like an inverse attraction. In a common attraction, the force is increasing with decreasing distance to the attractor. Here, we found less attraction closer to the trunk. Experience with objects and the egocentric body aura may play an important role for this effect. Objects are grasped and immediately taken to the egocentric body area for further inspection, but not too close to the body centre for handy

manipulation. Thirdly, the additional analysis with the data from the 2nd measurement showed that, presumably, the attraction of the body centre is stable, whilst additional tactile reference from the tip of the fingers shifted the errors distally. This peripheral drift by the additional touch at the fingers is stronger in the visual response mode.

In the light of self-protection it is interesting to note that a touch is experienced closer than it is actually applied – this might help protect us when we are touched by people or objects. The data also corresponds with the real life experience when small objects are taken closer to the body centre, the eyes, for visual inspection. In contrast, our arms have a much bigger radius of action. Finally, vision is highly sensitive to integrating additional tactile information. Recent studies showed that the egocentric body representation has multiple reference points. The present data did not replicate the influence of joints seen in previous studies (Cholewiak & Collins, 2003; de Vignemont et al., 2009; Parrish, 1897). In contrast, accuracy in tactile localisation linearly increased from the most distal to the most proximal stimulation point, from the palm to the forearm. The body centre has been found to act as a reference in other studies, namely for leg movements (Mouchnino et al., 1993) and arm movements, especially in expert dancers (see Experiment 4). Also, the head acts as a reference for rotations (Gentilucci et al., 1994).

To summarise, this study showed that sensory experience is highly modifiable. In addition to recent investigations, the data revealed that first, the perception of the body limbs and the sensory experiences were shifted, in the form of an attraction, by single or multiple reference points as it was the case in the sensory modality of touch, and that second, the pattern of the bias remains

constant while the direction of the experienced sensation or the mismatch in localisation is dependent on the task and the experience. For example, consider tactile sensitivity: Localisation is always bound to the body, which changes its size and form during development. The sense of touch is active from the very first moment in life (and before). To consciously experience touch and localise it as accurately as possible, tactile information is integrated into a representation of the body. The body representation and therefore tactile sensation has to 'grow' with its body. Moreover, it is well known that the resolution in touch perception can be increased by extensive training. For example, in severely visually impaired or blind people, the sense of touch superimposes visual perception. These findings together with the experiment above support the assumption of highly modifiable perception in the tactile sensory system.

Summary

Different studies have suggested that the body representation is segmented into its parts with the joints acting as landmarks. In this study, the representation of the body has been investigated by tactile experience across the wrist. Participants had to localise where they thought they were being touched. The participants significantly underestimated the distance at all locations from the body centre to the tactile location, whether they were pointing or whether they indicated the tactile location visually by naming the location on a superimposed ruler. The more the peripheral participants were touched, the bigger the proximal bias. However, a few participants showed a clear overestimation in localisation which resulted in a distal bias. Moreover, the results from retesting a subset of these participants revealed an underestimation in the tactile location according to

the group's mean. All of these participants had very long hands. While retesting these participants, it became evident that they supposedly touched the end of the box in the primary measurement. Thus, the response mode did not affect the bias significantly whereas – observed by coincidence – additional experimentally unintended tactile stimulation from the tip of the fingers resulted in a reversed bias. Therefore, the body centre acted as a reference point in tactile localisation only in those cases where the fingertip of the left arm did not touch the end of the box. Furthermore, in each the proximal and distal mislocation, the bias was bigger the more peripheral participants were touched. The body representation based on tactile sensation is body centred; additional tactile sensations were integrated as superordinate reference points; and independent of the sensory response mode.

The multisensory integrations in body representation based on tactile localisation (Experiment 5 in this chapter) were less effective than in the case of vision (Experiments 1 to 3 in chapter 2) or proprioception (Experiment 4 in this chapter). Nevertheless, other authors found alteration of the body representation in the tactile sense in response to movement (de Vignemont et al., 2009). This is of particular interest as the sense of touch is special in the case of information received from the external world. Therefore, it is of great importance to study the adaptability of movement representations, in particular the effect of different internal states. The adaptability in the movement representation is investigated in Experiment 6 (chapter 4). Two issues of motor representation adaptability were addressed by studying the effect of internal states in motor execution and motor imagery training.

Chapter Four

Movement Representation based on Imagery Training

Experiment 6: Learning a Novel Movement with Motor Imagery

Introduction

Athletes and artists use a diverse range of training methods to improve their motor performance. Thereby mental training techniques play an important role alongside general cardiovascular, strength, and flexibility training. Motor imagery of movement is one example of a mental technique. It has been referred to as conscious simulations of movement and consists of mental rehearsal of a movement without any motor execution. Other mental techniques feature the direction of the attention, such as focusing on the movements themselves (internal focus) or on the movement effects (external focus, effect anticipation, and feedback).

The effect of mental techniques on movement performance is not yet clear for imagery nor anticipation. Nevertheless, athletes themselves strongly believe in the benefit of mental techniques and use them irrespective of its efficacy (Cumming & Hall, 2002; Hanrahan & Salmela, 1990; Hanrahan & Vergeer, 2000/2001; Short, Tenute, & Feltz, 2005). For example, Hanrahan and Vergeer (2000/2001) compared dancers' self-rating with experts' rating in the height of the grand battement (rising working leg from hip into the air). The

authors found that dancers using imagery overestimated their performance and the effect imagery had (Hanrahan, 1995). Such strong beliefs in training techniques prime their regular use by sport athletes and other arts performers to improve movements that are already constituent parts of their motor repertoire as well as in learning new movements. However, no empirical evidence for the relation between particular mental techniques and specific performance effects when acquiring a novel movement has been demonstrated yet.

Performance changes due to imagery training have been measured in force gain, movement range increase, or movement accuracy improvement. Several studies showed that motor imagery enhanced performance of a movement that can already be performed (Blair, Hall, & Leyshon, 1993; Hanrahan et al., 1995; Mulder, Zijlstra, Zijlstra, & Hochstenbach, 2004; Yágüez et al., 1998; Yue & Cole, 1992; Yue et al., 1996; Zijdewind, Toering, Bessem, Van Der Laan, & Diercks, 2003). For example, Hanrahan et al. found that the use of specific mental images in preparation and during the execution of a movement increased the movement's accuracy, especially in particular, familiar dance movements. However, no general rule can explain the success of imagery on performance increase. Similarly, studies that focused on force increase by imagery training showed seemingly contradictory results. For example, participants in the study of Yue and Cole (1992) showed a significant increase in abduction force of the 5th digit after imagined isometric contractions in 20 sessions spaced across 4 weeks. However, Herbert, Dean, and Gandevia (1998) reported no significant increase in force after imagery training on easily executable movements, such as the flexion of the elbow. Type of imagery or mental technique, the biomechanical specificity of the type of movement, the

maximal muscle strength, the particular body parts involved, the level of the movements' representation, as well as the general imagery or movement skill level (expertise) are factors that are supposed to influence the degree of the obtained benefit. For instance, the effect of imagery on the actual movement performance measured in abduction amplitude was found to be dependent on the ability to execute the movement prior to imagery training (Mulder et al., 2004). Similarly, neuro-cortical changes based on motor imagery training were found to be dependent on the type of movement as well as on the extent of physical practice (Takahashi, Hayashi, Ni, Yahagi, Favilla, & Kasai, 2005).

Importantly, an increase in force is not necessarily related to an increase in muscle mass. The neuromuscular system adapts in response to imagery as well as physical training at different levels. Physical training can modify cortical maps, motor commands, descending drive, muscle activity, motor units, and sensory feedback as classified by Duchateau and Enoka (2002). Corcos, Jaric, Agarwal, and Gottlieb (1993), for example, showed that physical training changes the motor programs. Herein, the term 'muscle strength' is only used when an increase in force is related to an increase in muscle mass by extended muscle activity. In imagery, corresponding muscles are not supposed to be actively contracted; therefore, peripheral adaptations are unlikely. Jacobson (1930) and others (e.g., Bonnet, Decety, Jeannerod, & Requin, 1997), however, measured neuromuscular activity using Electromyographic (EMG) whilst participants were imagining. This peripheral activation led to the suggestion that imagery activates descending pathways and the corresponding muscles below threshold. The neuromuscular system was therefore assumed to be modified by imagery which can result in changes in the movement when executed. Nonetheless,

performance increase by imagery training could be shown even in cases where EMG inactivity during imagery was controlled (Yue & Cole, 1992), thus showing evidence in favour of imagery as a purely central mechanism. Furthermore, Yue et al. (1996) found an increase in force despite muscle atrophy, suggesting that muscle activation in imagery was unlikely. In addition, an imagined movement showed cortical activity similar to the actual execution of a movement (Lotze et al., 1999). Imagery training revealed enlargement of motor areas and a decrease in threshold activation by TMS after 5 weeks of imagery training akin to the central changes observed by physical training (Pascual-Leone et al., 1995). However, in a recent fMRI study by Nyberg, Eriksson, Larsson, and Marklund (2006) the brain activity was distinct for the imagery group compared to the performance group.

The neuromuscular stage of a movement is crucial for imagery training effects. For example, movements may be differentially affected by motor imagery when they are established in the motor repertoire (i.e., those with a consolidated motor representation) compared to novel movements. Healthy participants can generally access a motor representation of a movement consciously. Few novel movements can be considered purely novel. Most studies investigating the effects of imagery training on movement learning actually studied the effects on learning a new movement sequence, such as sequential control of individual finger movements. It is only recently that studies on motor imagery training in learning novel movements have been conducted on healthy participants (Mulder et al., 2004) and on relearning a movement in stroke patients (Carey et al., 2004; Dickstein, Dunsky, & Marcovitz, 2004; Dijkerman, Ietswaart, Johnston, & MacWalter, 2004; Gaggioli et al., 2004; Johnson-Frey, 2004; Liu, Chan, Lee,

& Hui-Chan, 2004a, 2004b; Malouin, Richards, Doyon, Desrosiers, & Belleville, 2004). Furthermore, the perceptual contribution in learning movements without any accessible motor representation has rarely been investigated. Some authors have suggested that movement observation and imitation play a particular role in learning how to perform a novel movement (e.g., Mattar & Gribble, 2005). Nevertheless, it remains unclear to what extent and on which level in the nervous system motor imagery is involved in these processes (e.g., Clark, Tremblay, & Ste-Marie, 2004; Duchateau & Enoka, 2002; Jeannerod, 1995; Vogt, 1996).

In order to receive a clear image of the impact of motor imagery training, all possible bodily and cognitive constraints have to be considered. The present investigation was designed to gain further insight into the processes of imagery by studying imagery effects on a novel movement which has never yet been executed in daily life. In correspondence with Mulder et al. (2004) the continuous abduction movement of the big toe was taken for the investigation as a novel movement. The abduction of the big toe is a special movement in several ways. First and foremost, many people have difficulties making an abduction movement of their big toe although they can quite easily flex or extend it. The joint at the big toe is unique with respect to anatomical mechanisms compared to joints at the other toes (Coughlin, 1996).

The learning effects in this experiment are of interest for several reasons. Recent studies investigating imagery training found different effects of expertise (e.g., Driskell, Copper, & Moran, 1994). Mulder et al. (2004) investigated the imagery effect on the abduction of the big toe and found improvement only when the participants could execute the abduction prior to the training. However, in contrast to Mulder et al., the force increase was measured in addition to the

abduction amplitude. If imagery training and physical training have distinct neural correlates, differences in the performance other than force or movement range extension should be observable. Therefore, time parameters were also considered separately in the force measurement to look at changes in maximum force, maintaining force, and the onset of movement. The additional measurement of the isometric contraction also allowed measuring low level of muscle activity.

Based on the findings of previous studies, an increase in maximum force and maintaining force was proposed to be biggest in response to execution training. Previous studies on imagery training have not included time considerations such as the rate of force development. For example, in several athletics disciplines, such as sprint or javelin, the rate of force development and the onset of movement are of great importance in competition. Kimura, Imanaka, and Kita (2002) found that the onset of movement is mediated by mental factors rather than by the effects of peripheral muscular preparation. It is expected that mental imagery training decreases the onset of movement over the training sessions. Furthermore, a comparison between dancers and nondancers allowed identification of potential differences in mental imagery and movement abilities in the individual. An understanding of how motor commands can be built, accessed, and modified, particularly by using deliberate imagery, is essential for sport athletes and may foster programs for motor rehabilitation.

Method

Participants

The participants were recruited at the University of Zurich and at a training and performance centre for professional dancers. Eight undergraduate students and 10 professional dancers participated in this study. All participants gave written informed consent to participate in this study, which was performed in accordance with the Declaration of Helsinki. The participants received written instructions explaining the task and the procedure. The participants (3 male, 15 female) were tested individually in a quiet room. The mean age was 29.0 ± 6.1 years. All participants were right handed according to Briggs Handedness Questionnaire (Briggs & Nebes, 1975). According to Maupas, Paysant, Datie, Martinet, and André (2002) each possible aspect of footedness was tested (stability, accuracy, and dynamic). All but 2 participants had an overall dominance of their right foot and all participants had a dominance of fine motor activity on the right foot (grasping an object). Participants were paid for their participation and they had never taken part in any similar study. The dancers' interest was motivated by their knowledge about the importance of the feet's stability for balance (Mann & Inman, 1964) and the big toe's involvement in movement precision (Howse, 1983). None of the participants received any training of the big toe prior to the participation in this study. Only participants who reached an overall rating score in the Vividness of Motor Imagery Questionnaire (VMIQ, Isaac et al., 1986) for the kinesthetic imagery of 70 or less (possible range, 24-120; best score 24) and participants without previous muscular and skeletal injuries or pain of the lower limb were included in the analysis.

Design

In order to investigate the effect of motor imagery on novel movements, a learning experiment with a between-subjects design was chosen. Participants had to learn the abduction movement of the big toe by repeated isometric contractions of the abductor hallucis. The groups performed different training tasks. Those were imagery, execution of the big toe, or execution of a control movement. Each participant was assigned to one training group prior to the first training. Each group consisted of 6 participants; the groups were approximately balanced for age, gender, and expertise in dance.

The measurements and the sessions' procedure were the same for all participants with one measurement phase before, one after the training phase for six sessions during 2 consecutive weeks. Each week consisted of a session on Monday, one on Wednesday, and one on Friday. As illustrated in Table 6 (p. 137), each session included a training phase and two measurement phases, the abduction amplitude (referred to as amplitude), and abduction force (referred to as force). Each session started and ended with the amplitude measurement once in each condition, visual anticipation, and eyes closed. The force was recorded 5 times before and 5 times after the training phase.

The training phase consisted of 15 repeated movements of either the executed or imagined abduction of the big toe on the right foot or a control movement of the right hand for each group. One session lasted approximately 16 min for the experimental phases (training and measurement phases), plus approximately 15 min of preparation prior to the experiment (questionnaire, disinfection, and foot massage).

Equipment

The participants were seated in a chair with their knees flexed at approximately 110° and their right foot fixed in the apparatus. A light and tone device on the table indicated the pace of the abduction movements. The testing apparatus consisted of an iron plate on which the two levers necessary for the measurements were attached solidly by strong magnets inserted on their lower side. As illustrated in Figure 15 (p. 137), a separate lever was used for the amplitude and for the force, respectively. The apparatus was positioned against an obstruction bar to provide stabilisation. The feet of the participants were positioned on disposable drapery and the small toes were fixated so that they would not move. Additional pieces of felt were used to provide comfortable but sustainable fit. It was important that the participants concentrated on the movement of their big toe without having to ensure stabilisation of the foot.

The lever for the measurement of the amplitude was movable. The corresponding muscle for the abduction originates from the tuber calcareous (heel). For that reason the torque of the moveable amplitude lever was at the level of the tuber calcareous, thereby providing a larger radius for more precise measurements (scale ranging from -6.0 to 41.0 mm, resolution 1 mm). The lever was adjusted at the height of the cuticle of the big toe. The big radius provided a better abduction measure. The lever remained still at the maximally reached amplitude.

The lever for the force was stiff. The force lever measured the applied force isometrically. The force was recorded by means of an analogue force sensor with a piezoresistive micro-machined silicon sensing element (HONEYWELL, MICRO SWITCH Force Sensors, http://sensing.honeywell.com) adjacent to the back end of the lever. The muscle contraction was thus nearly

isometric (maximal abduction forces yielded a 1 mm displacement of the lever). The applied force was measured in newton (N) continuously (low linearity errors ± 0.5% span, range between 15 and 55 N maximum), amplified and converted to a binary signal (8 bit resolution). The maximum force at the sensor was set to 10 N with a resolution of 0.04 N. A microprocessor connected to an IBM DOS by a serial port processed optic, acoustic and force signals at a sampling rate of 31.5 Hz.

Tasks Procedure

The movement was explained in detail to all participants. Then, they were asked to make a flexion and extension of the big toe. Subsequently, all participants were instructed to passively abduct the big toe by pulling down along the medial side of the foot with the forefinger to experience to abduction movement. Furthermore, it was explained to the participants that people are usually not able to execute this movement from the very beginning, and they were encouraged to try. After disinfection of the foot, participants received a 10 minute relaxing massage on the right foot in order to attain a standard level of muscle tonus before the experiment started. The participants' right foot was then fixed onto the measurement apparatus with Velcro fastener. Pictures of the fixed foot were taken before the measurements to ensure identical positioning in the consecutive sessions.

Table 6.

Experimental Procedure in Minutes for Each Participant in Each Session of Experiment 6.

	Pre-training Measurement			Training	Post-training Measurement		
Activities	Amplitude	*Change to Fixed Lever*	Force	Execution, Imagery, or Control	Force	*Change to Moveable Lever*	Amplitude
Duration	~ 1	~ 1	2.145	7.8	2.145	~ 1	~ 1

Timeline (min)

Note. Each session started with a pre-training measurement where first the amplitude was measurement with the moveable lever. For the force measurement, the lever needed to be changed to the fixed lever, and vice versa in the post-training measurement. ~ = Approximately.

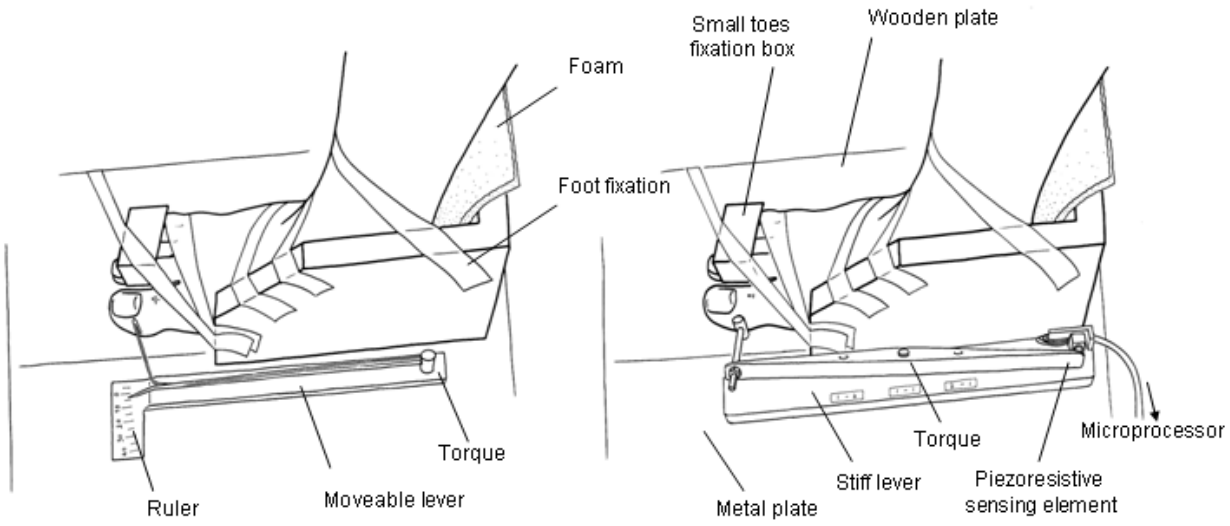


Figure 15. Experimental apparatus with foot fixation and measurement levers. Left image: movable lever for abduction amplitude with scale in millimetres; right image: stiff lever for abduction force measurement in newton.

Training Phase

The participants' foot rested in the apparatus throughout the entire session. The force training phase consisted of repeated presses and relaxations in the execution and mentally rehearsed presses and relaxations in the imagery group, respectively. The control group trained the 'Mister Spock' finger sign with the right hand (i.e., abduction of the 4th and 5th finger together with adduction of the middle and index finger). Participants in the execution group had to press against the lever as strongly as possible with their big toe and then relax. Participants in the imagery group were instructed to imagine pressing with their big toe against the lever without actually making any overt movement or muscle contraction. They were told to imagine the movement as vividly as possible while keeping the foot muscles relaxed. The experimenter supervised the force values on-line presented on a computer screen to ensure the absence of any movement for the imagery and the control group. The number of repetitions (15) and the frequency of the repeated executed or imagined movement was equal in all groups. Participants were prepared for the press by a preparatory signal (double beep) 3 s before the signal to press. A green light indicated the press phase (7 s). Participants relaxed for 20 s before the next trial. In the imagery group, the light signals were replaced by a single beep for press and a prolonged beep for relaxation.

In the training phase during actual pressing or imaging, respectively, all participants were interrupted randomly three times at one of six time points (1-6 s after press) by a double beep. They were asked to rate their sense of effort at the moment of the interruption on a scale ranging from 1 (*low*) to 5 (*high*). This subjective rate of effort was used to control for the mental activity of the imagery group.

Measurement Phase

The amplitude was measured under two perceptual motor control conditions administered in randomised order for all participants. In the perceptual motor control condition the participants had to press with their big toe against the moveable lever whilst looking at the point of the scale where they wanted the lever to go, thus visually anticipating the goal of the movement and receiving visual feedback of their actual performance. In the eyes closed condition the participants had no visual feedback during the movement. In each condition, the amplitude was measured once before and once after the training phase (four amplitude measures per session). The investigator inspected the scale and noted the size of the abduction. The perceptual control condition was included from the 2nd session on as the experimenter observed striking differences in the 1st testing session.

For the force measurements, each participant had to press against the stiff lever for 4 s and then relax for 3 s. This sequence was repeated four times pre- and four times post-training (i.e., four repetition trials, eight force measurements per session). Participants received a preparatory tone signal (double beep) 1.5 s before the red light signal indicated data collection. After 3 s a green light was switched-on for 4 s initiating the press phase and the subsequent relaxing phase when it was switched-off. As long as the red light was on for another 4 s the measurement was progressing. The pause between presses was 10 s.

Analysis

The collected force data were imported into Vision Analyzer (BRAIN PRODUCTS GmbH, Brain Vision Analyzer Version 1.5, http://www.brainproducts.com) with the

generic data reader and manually typed marker files. The raw data were automatically segmented in slices of 11000 ms length, baseline corrected to zero (-1500 ms before start). Peak detection, exerted force, and the integrated surface underneath the force curve (Ns) of the averaged repetition trials were exported for further analyses.

Firstly, the initial amplitude and force values were assessed to test for individual differences prior to the experiment. The initial values were defined as the first trial in session 1. Then, training induced changes in amplitude and force were tested for statistical significance in SPSS Version 11. Significant training induced changes were tested as significant increases in performance with respect to the participants' 1st session (e.g., session 2-1, session 3-1, etc.) and by significant increases between sessions (e.g., session 2-1, session 3-2, etc.). Repeated measures analysis for the within-subjects factor session and the between-subjects factor group were conducted. Differences between groups for a specific session and differences within groups were further analysed with contrast analysis as well as paired samples *t* tests. In order to assess for significant ordered differences (e.g., retention force increases over training sessions) the nonparametric Jonckheere Terpstra test (JT; Jonckheere, 1954) was conducted. The sample was also tested for normal distribution in abduction amplitude and force performance with one-sided Kolmogorov-Smirnov Z (K-S Z). The values in the text are given as mean (*M*) ± standard deviation (*SD*) in millimetres for the movement amplitude and in newton (N) for the force (analyses with the median showed equivalent results).

Results

Of the 18 participants, 4 participants had to be excluded. One of these participants had an initial force peak higher than 2 x *SD* above the overall mean and was therefore considered as an expert in executing the abduction movement. Another participant had a hallux valgus angle around 35° which made a reliable adjustment of the levers impossible. In addition, 2 participants had long-lasting pain or a severe operation at their lower limb. Therefore, the groups consisted of 4 participants in the imagery, 4 participants in the execution, and 6 participants in the control group.

No differences were found between the dancers and nondancers; they were thus pooled together for further analyses. Furthermore, no significant differences within a session, that is, before versus after the training, was found. Each session's performance was therefore computed by averaging the repetition trials before the training phase ignoring the trails after the training phase. This means that the first two values for amplitude or the first four values for force were merged at each session.

Abduction Amplitude

The movement range of the abduction was measured by the amplitude in millimetres. The mean values for each session with and without vision are listed in Table 7 (p. 147/148). None of the participants had an initial amplitude of zero; the minimum amplitude was 3.0 cm and the maximum amplitude was 17.5 cm. The overall mean initial amplitude for all groups was 7.7 ± 4.0 and did not differ from a normal distribution, $p = .63$, K-S Z. The initial amplitude did not differ between groups, $F(2, 11) = 0.40$, $p = .71$, and equal variances could be

assumed, Levene Test for Variance Homogeneity, $F(2, 11) = 0.42$, $p > .10$. A three-way ANOVA with the within-subjects factors perceptual control (visual anticipation vs. eyes closed) and amplitude change (session 2-1 till session 6-1) and the between-subjects factor training group (execution vs. imagery vs. control) revealed a significant main effect for the within-subjects factors perceptual control, $F(1, 11) = 16.10$, $p < .05$, and amplitude change, $F(4, 44) = 7.12$, $p < .001$. The amplitude showed a significant linear increase with bigger changes for later sessions, $F(1, 13) = 26.22$, $p < .001$. Perceptual control led to significantly higher a changes compared to eyes closed (0.41 ± 3.14 vs. -.10 ± 2.77) in a two-tailed paired *t* test, $t(13) = 3.59$, $p < .05$. The factor training group was not significant, nor did any interaction with training group reach significance (all *p*'s > .25).

Figure 16 (p. 143) displays the amplitude changes (session 2-1 till session 6-1) for the three training groups. The decrease in amplitude from session 1 to session 2 is not significant. As illustrated in the figure, session 3 showed a clear increase in amplitude change in contrast to session 1 but for the execution group only. With respect to this observation, one-tailed *t* tests were conducted. The analysis showed a trend towards higher amplitude changes for the imagery than the control group at session 5 with respect to the 1st session, $t(8) = 1.26$, $p = .12$, and a higher amplitude increase for the execution group compared to the control group at session 6 in respect to session 1, $t(8) = 1.86$, $p = .05$.

Abduction Force

With respect to the analysis of force, three movement dynamic parameters were analysed; reaction time, exertion force, and the rate of force change. All three

parameters were based on the force onset, which was defined as the first 0.04 N increases after the starting signal followed by a continuous increase in force. The reaction time (ms) was the time between the starting signal and the force onset. The exertion force (Ns) was defined on the basis of induced force curves over the first 2 s from the force onset. The rate of force change, N(*t*), was obtained by the first derivative, N(*t*) = dN/d*t*, calculated from the force onset to the peak force reached in 1.4 s.

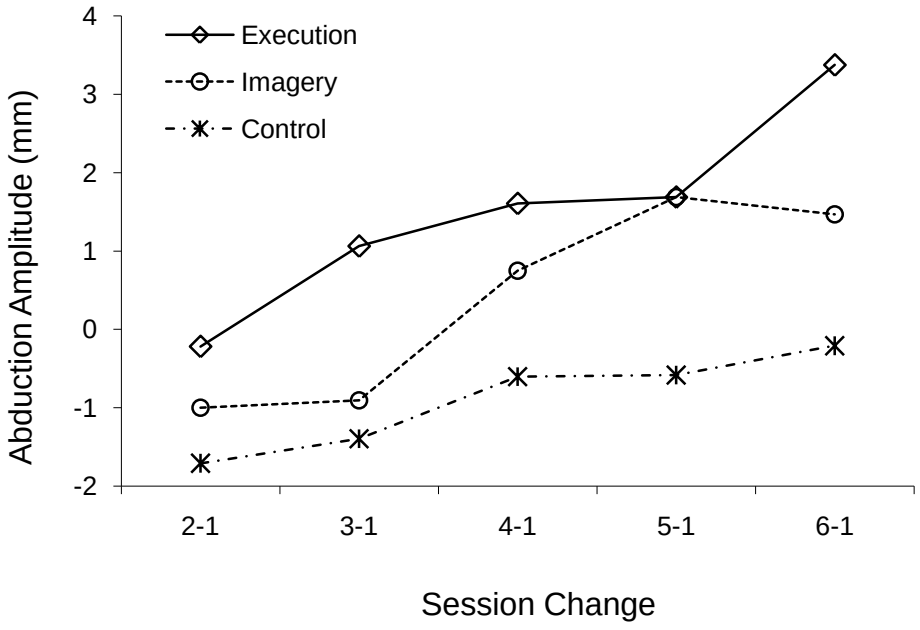


Figure 16. Mean abduction amplitude for execution (n = 4), imagery (n = 4), and control (n = 6) training groups of Experiment 6 over six training sessions. X-axis: session measure, changes in abduction amplitude are indicated as individual differences to the 1st measurement for each subject, that is, from measurement session 2 to session 6 each with respect to the subjects' 1st session; y-axis: mean abduction amplitude in millimetre.

Exerted Force

The mean initial exertion force (Ns) of the 1st abduction was 452.94 ± 489.77 for all participants together and did not differ significantly from a normal distribution, K-S Z, p = .31. The difference between the groups for the initial exertion force was not significant, $F(2, 11) = 0.47$, p = .63, Levene Test for Variance Homogeneity $F(2, 11) = 2.63$, $p > .10$. None of the participants had zero exertion force, min = 9.49, max = 1785.08.

Figure 17 (p. 145) displays the mean force curves for each session for the execution and the imagery group only. A clear increase in exerted force from session to session can be observed in the imagery group. The execution group showed a similar increase in force, unless between sessions 3 and 4. A test for the order of continuously increasing exertion force over the six sessions was significant for the imagery group only, JT, $p < .05$.

The ANOVA for the within-subjects factor exertion force change (session 2-1 till session 6-1) and the between-subjects factor training group (execution vs. imagery vs. control) revealed a significant main effect with increasing force change, $F(4, 8) = 3.80$, $p < .05$. The between-subjects factor group showed a nonsignificant trend, $F(2, 11) = 2.28$, p = .15. The independent one-tailed t test revealed a significantly higher mean increase in force change in the execution (628.46 ± 351.46) than in the imagery group (72.87 ± 284.45), $t(6) = 2.02$, $p < .05$. The execution group also showed a strong tendency for a higher mean increase in force change in contrast to the control group (298.38 ± 308.35), $t(8) = 1.57$, $p < .08$. Differences between imagery and control did not reach significance.

Differences of force changes were compared within each training group. The one-tailed paired t test showed a significant increase in the mean exerted

forces in the execution group compared to session 1 in session 3, $t(3) = 2.61$, $p < .05$, session 4, $t(3) = 3.41$, $p < .05$, session 5, $t(3) = 5.32$, $p < .05$, and session 6, $t(3) = 3.28$, $p < .05$. The imagery group showed a significantly stronger exertion force at the last (session 6) compared to the 1st session only, $t(3) = 2.60$, $p < .05$. The control group showed significant differences to session 1 at session 3, $t(5) = 2.75$, $p < .05$, and session 6, $t(5) = 2.49$, $p < .05$.

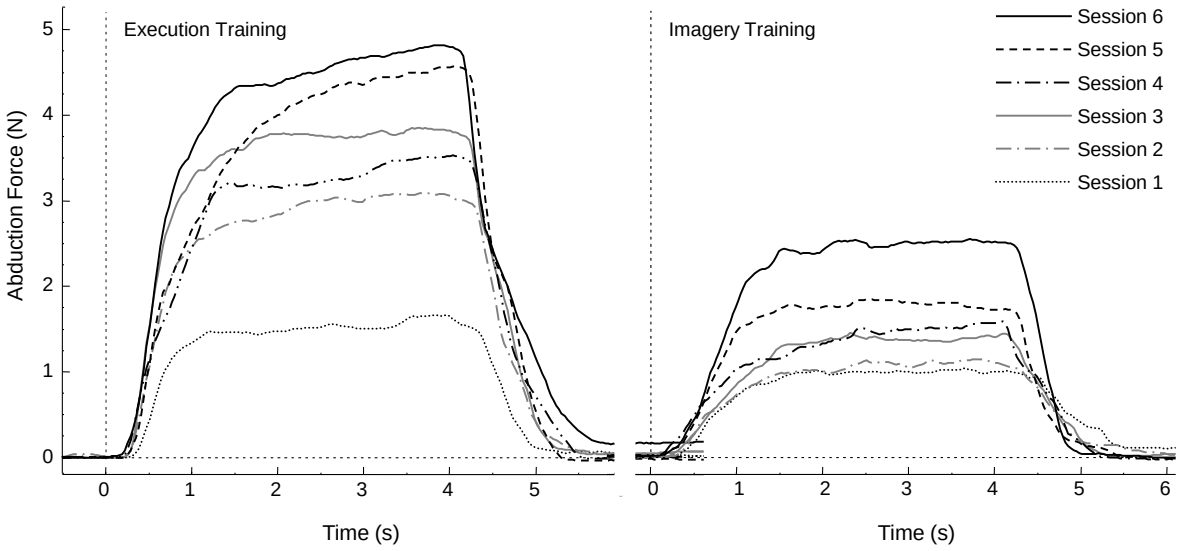


Figure 17. Mean force curves for execution and imagery group over 6 measurement sessions of Experiment 6 for each session separately (n = 4 for each group). X-axis: session measurements 1 to 6, with signal to press (dotted vertical line that crosses x-axis at zero); y-axis: mean force curves in newton (N).

Reaction Time

Statistical analysis with the within-subjects factor reaction time changes (session 2-1 till session 6-1) and the between-subjects factor training group (execution vs. imagery vs. control) revealed a significant main effect in reaction time change with a decrease over sessions, $F(4, 8) = 2.81$, $p < .05$. The between-subjects

factor training group did not show a significant main effect. However, as can be seen in Figure 18 (p. 147), the imagery group showed a clear decrease in reaction time. Therefore, within-subjects contrast analyses for the training groups were conducted separately. These analyses showed a significant linear decrease over sessions in reaction time for the imagery group only, $F(1, 3) = 16.65$, $p < .05$. In contrast to reaction time before training at session 1 tested with one-tailed paired t tests, the reaction times of the imagery group decreased significantly at session 3, $t(3) = 5.20$, $p < .01$, session 5, $t(3) = 4.06$, $p < .05$, and session 6, $t(3) = 3.30$, $p < .05$.

Rate of Force Change

The univariate ANOVA with the within-subjects factor dF/dt change (session 2-1 till session 6-1) and the between-subjects factor training group showed a significant main effect for dF/dt over sessions, $F(4, 8) = 2.89$, $p < .05$. One-tailed paired t tests showed that the increase in dF/dt from session 6 with respect to session 1 was responsible for the main effect, $t(13) = 2.21$, $p < .05$. The between-subjects factor training group did not show a significant effect.

Relationship between amplitude and force measures

Given the increase in both the amplitude and force, as described above, could lead to the assumption that these parameters are dependent. Correlation between amplitude (mean of all trials from a given session) and force (exertion force area of all trials before the training phase) are displayed in Table 7 (p. 147/148). However, significant correlation was identified for the control group only. For both the imagery and execution group, changes in amplitude and force seemed to be independent of each other.

Sense of Effort

The subjective effort ratings showed a significant increase with higher ratings at later time points for all three groups, execution, JT $p < .05$, imagery, JT $p < .001$, and control, JT $p < .05$.

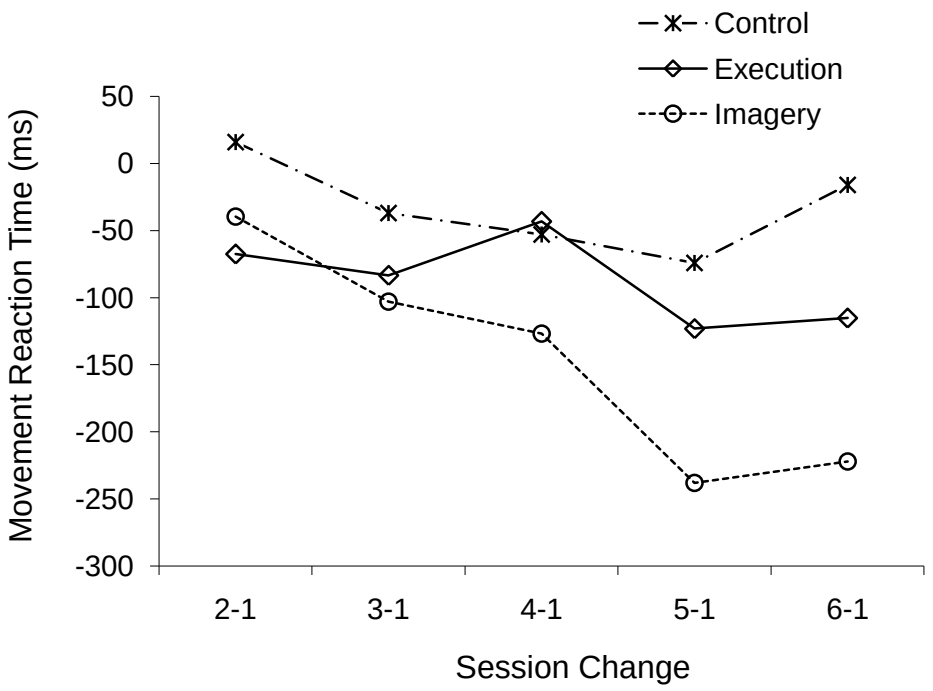


Figure 18. Mean movement reaction times for execution (n = 4), imagery (n = 4), and control (n = 6) training groups of Experiment 6 over six training sessions. X-axis: session measures indicated as changes in reaction time over the 6 training sessions are given as individual differences to the 1st measurement for each subject, that is, from measurement session 2 to session 6 each with respect to the subjects' 1st session; y-axis: mean movement reaction time in milliseconds

Table 7 (next page).

Correlation Analysis of the Mean Abduction (trials before and after the training phase) and the Mean Force (trials before the training phase) for Each Session (session 1 to session 6) of Experiment 6.

Group	Session	r	Abduction (mm)	Force (N)
Control[a]	1	.70	6.27	474.30
	2	.93***	6.25	562.82
	3	.88*	6.93	860.84
	4	.94**	7.26	619.93
	5	.89**	7.59	866.56
	6	.85*	8.27	953.25
Execution[b]	1	.83	5.53	502.76
	2	.65	6.56	848.79
	3	.67	7.78	1352.11
	4	.27	8.38	1021.95
	5	-.11	8.77	1042.25
	6	.37	9.58	1390.99
Imagery[c]	1	.29	7.61	298.26
	2	-.10	7.39	313.93
	3	.40	7.83	404.55
	4	.03	8.82	449.49
	5	-.50	10.25	534.22
	6	.54	9.95	653.47
All Subjects[d]	1	.50*	6.44	432.14
	2	.52*	6.67	573.42
	3	.53*	7.43	870.83
	4	.48*	8.02	686.10
	5	.47*	8.69	821.80
	6	.52*	9.13	992.67

Note. [a]$n = 6$. [b]$n = 4$. [c]$n = 4$. [d]$n = 14$. *$p < .05$, two-tailed. **$p < .01$, two-tailed. ***$p < .001$, two-tailed.

Discussion

It is well known that appropriate training results in strength increase of the trained muscles. Thus, sport athletes and recently also professional dancers (Wyon & Redding, 2005) follow systematic fitness training including physical and mental training in combination with careful assessment, goal determination, regularity, and evaluation. However, physiological and neuronal effects of various training forms are still debated and most training studies have been conducted on already established movements. If we were aware of the factors allowing movement improvements via mental imagery training to happen, imagery could be used more efficiently in sports as well as in rehabilitation as for example with stroke or neglect patients. In this study, performance effects of execution and motor imagery training on the abduction of the big toe and a control group who physically trained the 'Mister Spock' finger sign were compared. For most people, it is very difficult to abduct the big toe; the concurrent motor command – if existing after all – cannot be easily accessed. The data showed two specific central effects. First, imagery reduced movement reaction time, and second, sensory afferences gained from visual feedback were taken into account during motor execution.

The data in this study revealed significant training effects in exertion force, reaction time, rate of force change, and in the abduction amplitude of a novel movement over 6 sessions, although none of these movement parameters showed an immediate effect of training within a session (i.e., comparing measurements before with after a training session). Therefore, assessing a motor command of a nonestablished movement can improve with a small amount of repetition trials. Differences between the training types were restricted. A lack of

a significant difference between the three training forms can be explained as follows: First, for an improvement in performance rather than muscle mass increase neuronal changes are necessary. Second, all training groups have to rely strongly on motor imagery when trying to execute such a novel movement. This means that motor imagery and neural adaptations played an important role in all three groups. This is supported by several studies demonstrating that force increase during the early phases of strength training is provided by neural changes (Enoka, 1988; Gabriel, Kamen, & Frost, 2006; Moritani & deVries, 1979; Sale, 1988).

Abduction Force and Reaction Time

A striking result is that execution compared to imagery or control showed a trend for an increase in exertion force whereas only imagery showed a significant decrease in the reaction time. Therefore, participants in the imagery group learned to execute the abduction movement significantly quicker compared to the execution or control group whereas the execution training showed the biggest exertion force increase. The activation of motor neurons in the training phase was specific to the execution group. Thus, neural adaptations respond in a specific way with or without repeated muscle contraction.

The advantage of execution over imagery training in exertion force corresponds with other studies that investigated the effects of imagery. However, in contrast to other studies, execution and imagery training did not show significant training effects compared to the control group (Yue & Cole, 1992; Zijdewind et al., 2003). Although initial differences between the groups were not significant, it has to be highlighted that the lowest initial exertion force was observed in the imagery group. The unexpected increase in the movement

performance for the control group has been reported elsewhere (Herbert et al., 1998; Zijdewind et al., 2003). In this study, the control and imagery group executed the abduction movement of the big toe 8 times per session, which amounted to 42 times in total. Therefore, it seems that relatively little training of the abduction movement resulted in a clear effect of the movement performance. Although the imagery and the execution group showed some changes over and above those found in the control group, all groups had enough execution trials in the measurement phases to train the abduction of the big toe. The fact that the abduction movement of the abductor hallucis can be trained even by a very small number of trials below training threshold has considerable therapeutic relevance.

Abduction Amplitude

Evidence for a clear impact in the abduction amplitude was observed in both anticipation and training. The amplitude was consistent bigger in the visual anticipation condition and repeated abduction training led to a linear increase in amplitude from session 1 to session 6 in all three groups.

In the last session, participants who trained the abduction by execution showed significantly bigger amplitude increases compared to the control group. It is unclear whether additional training sessions would have revealed greater differences between the training groups. Interestingly, in all training forms, the amplitude showed a nonsignificant reduction after the 1st training session compared to the initial abduction movement. The range of a movement is clearly related to biomechanical limits (Coughlin, 1996). Unfortunately, the passive range of motion was not measured. Knowledge about the absolute passive range of the abduction movement would allow indicating possible ceiling effects. Nevertheless, the visual focus of moving the lever through its maximum rendered

an increase in maximum amplitude which was significantly beyond that obtained with eyes closed. This is in line with other studies that showed enhancement in motor learning and rehabilitation when directing the focus on external effects, whilst ignoring the body-inside (Wulf & Prinz, 2001). Consistent with this, Graves and James (1990) showed that visual feedback has an impact on the force of unfamiliar movements. The central nervous system uses visual information for feedback-based control of precision grasping movements (Paulignan, Frak, Toni, & Jeannerod, 1997), force production (Slifkin, Vaillancourt, & Newell, 2000), and motor learning (Wulf & Prinz, 2001). However, in addition to the aforementioned studies, visual feedback was shown to increase the performance of a single movement, thus providing further evidence that both sensory afferences and motor imagery are involved in motor planning (Decety & Jeannerod, 1996). Motivation was not responsible for the bigger amplitude in the eyes open condition because participants noticed their performance increase in the anticipation condition themselves and expressed high motivation to beat their maximum in the eyes closed condition.

These results are not consistent with those of Mulder et al. (2004). For some of the participants, the authors reported initial abduction amplitude of zero while all participants in this study showed some minimal abduction force and amplitude. The experimental apparatus in this study was very sensitive and could detect very small changes. None of the participants in this study had zero degree abduction amplitude or zero retention force at the 1st abduction measure. Zijdewind et al. (2003) found similar effects on the abduction force increase with imagery training. The authors showed a significant effect of imagery after the 5th week of imagery training of the ankle plantar flexor muscles. These muscles are

much stronger than the abductor hallucis and participants in the current study only trained over a 2-week period. The amount of training for the abduction movement in our experiment might not have been enough to reveal any group differences.

Duration, Retention, and Expertise of Motor Imagery

The results revealed new effects of imagery and are in contrast with previous studies on imagery training (Driskell et al., 1994). First, no immediate training effect could be detected. Second, imagery training led to a continuous increase in exertion force, whereas physical practice led to a clear decrease after the 2-days rest period at session 4. The 4th training and measurement session was the only one with a 2-day rest period from the previous session (weekend between session 3 and 4). It is notable that the pause had no effect on the force increase for the imagery group. Thus the changes induced by imagery seemed to sustain across longer resting periods. However, the maximum force is higher in the execution group. It is possible, that the higher the maximum muscle strength, the harder it is to maintain the force level (i.e., the more sensitive to reversibility). Nevertheless, the constant force increase found in the imagery group looks as if it might reach the same level as the execution group after a bigger number of training sessions. If this is true, in situations where strength cannot be trained constantly, imagery training might maintain force increases over time. Third, neither imagery expertise effects between dancers and nondancers nor effects of training between groups were significant.

Reaction Time

Increase in the speed of voluntary muscle contraction is accomplished by neural adaptations such as changes in the firing pattern of motor unit activation (Van Cutsem, Duchateau, & Hainaut, 1998) or the greater recruitment of fast twitch type motor units (Kauranen, Siira, & Vanharanta, 1998). Therefore, imagery training clarified and specified the motor command. However, without EMG activity, it cannot clearly be ruled out whether the reduction in reaction time is due to central (premotor time from a go signal to EMG activity) or peripheral changes (motor time corresponding to muscle contraction, time from EMG activity to movement, Weiss, 1965). Nonetheless, central processes such as attention or fatigue cannot be the main cause of faster responses. First, in correspondence with Panton, Graves, Pollock, Hagberg, and Chen (1990) differences in reaction time between control and execution could not be found. Therefore, the lack of decrease in reaction times in the execution group cannot be due to fatigue effects as also previously shown by Kauranen, Siira, and Vanharanta (1999). Second, there is no evidence for attention differences across the three groups.

Force and Abduction Amplitude Correlation

The correlation between force and amplitude of the big toe remains significant only without training. This finding supports the idea of further underlying neuromuscular changes by execution and imagery in contrast to the control group and it shows the relevance to compare several movement parameters.

In contrast to previous studies, the percentage of maximal voluntary contraction was not acquisitioned (Allen, Gandevia, & McKenzie, 1995; Herbert et al., 1998). The voluntary force activation of the trained elbow flexor muscle in the study by Herbert et al. was close to its maximum before training. In contrast, Zijdewind et

al. (2003) supposes that the ankle plantar-flexor muscles are difficult to activate maximally so that imagery training could enhance the neural drive during a maximal voluntary contraction. This is congruent with this study where the abduction of the big toe is difficult to execute.

Sense of effort

The participants' own rating of effort increased linearly with the time from pressure to the rating interruption (between 1 s and 6 s after start to press) whether they imagined or executed the movement. This linear similarity in sense of effort in the execution and the imagery group indicates the high degree of mental activity in the imagery group. Alkadhi et al. (2005) found high correlations between self-rated imagery vividness and the degree of brain activation which was interpreted as reflecting neural correlates of the motor cortex process. Therefore, the assumption that the sensed effort reflects underlying cognitive processes is plausible.

The present study shows an impact on force and amplitude of the abductor hallucis with a small number of voluntary isometric contractions and abduction movements over the course of 2 weeks. The abductor hallucis is a long intrinsic muscle of the foot with a mean length of 115.8 mm (Kura, Luo, Kitaoka, & An, 1997; Mann & Inman, 1964). The contraction of the abductor hallucis is mainly responsible for the abduction movement of the big toe. The function of the abductor hallucis and its counterparts play a major role in the therapy treatment of hallux valgus, a painful deformity of the big toe (Coughlin, 1996). The abduction of the big toe therefore provides the possibility to study the effect of training on a novel not yet established movement, which is also important to provide proper alignment of the big toe. Furthermore, the study also showed that

the most effective way to execute a difficult movement is by incorporating sensory afferences through visual anticipation of an external event. Moreover, the greatest benefit for a reduction in onset of movement and the biggest resistance to decay gained retention force can be achieved by imagery training. Therefore, when considering movement rehabilitation, it is plausible to use imagery instead of execution to specify the motor command and to use perceptual control strategies to improve the actual performance at any stage of rehabilitation. However, it is necessary to acknowledge that particular movement parameters have to be considered when comparing effects of imagery with execution training.

Conclusion

With this investigation it could be shown that training of a nonestablished movement leads to neuromuscular adaptations which result in force and abduction amplitude increase as well as movement reaction time decrease within a 2-week training period. The specific effects of imagery training provided some insight into the neural adaptations when no efferent and afferent motor feedback is provided. Imagery training showed a low increase in isometric force and a clear decrease in reaction time from signal to move. Furthermore, the neural adaptation by imagery training was resistant to rest phases. This result therefore provides evidence that neural adaptations without motor feedback differ from those with motor feedback, mainly in the time course of accessing motor units. Without motor feedback in training, access of motor units can be learnt more quickly. Moreover, visual sensory feedback seems to have had an immediate effect. With visual feedback, the activated motor command to abduct the big toe lead to better performance. Further investigations involving techniques such as

twitch interpolation or EMG are necessary in order to allow inferences about the particular neural adaptations. For example, the current data did not allow deducing whether changes in reaction times were due to an increase in neural firing rate or whether the amount of motor unit recruitment in a voluntary neural activation increased. Furthermore, it is not clear whether motor or premotor time was reduced.

For the first time, howere, it could be shown that there is evidence for a particular training effect after motor imagery. Imagery training only resulted in a decrease in reaction time whereas physical training revealed an increase in exertion force. Thus imagery and execution training differ in their level of performance and also in their particular performance dimensions. Imagery is not just less than execution, it is different, at least for a movement without a previously established motor command.

Summary

Recent research has provided evidence that repeatedly performed movements in the mind increases muscle force (i.e., Yue & Cole, 1992; Yue et al., 1996; Zijdewind et al., 2003). This experiment investigated whether motor imagery necessarily draws on already actively established motor commands. Participants trained the abduction of the big toe, a movement which is rarely executed in daily life, under various training conditions over a period of 2 weeks. A significant increase across all training sessions was found in abduction amplitude and abduction force, but no main effect for training was found. However, for the imagery group, the time of the movement onset linearly decreased. Furthermore, when participants visually anticipated the movement, they reached significantly

larger abduction amplitude. These results indicate that imagery does not rely exclusively on previously exercised motor commands and visual anticipation with feedback of an external effect also supports execution of an infrequent motor command.

Chapter Five

General Discussion

Summary Considerations

Each of the experiments discussed in this thesis showed evidence that body (chapters 2 and 3) and movement representations (chapter 4) are adaptable in short- and long-term. These findings and experimental measurements are summarised in Table 8 (p. 160) and outlined in the following subsections.

Representation Effects in Different Sensory Systems

1) Vision

The time needed to identify visually presented stimuli is taken as an indication for the transformation processes of the representations. These processes are dependent of the orientation of presented stimuli as well as of the representation form as shown in Experiments 1 to 3. First, identification showed little egocentric body transformation time costs when the body figure was presented upside down. Second, posture matching did not show such mental transformation costs when the matching posture was presented in Labanotation, an abstract symbol notation for dance. This means, egocentric body transformation is adaptable with respect to both the representation level and orientation of the visually presented body stimuli in short-term.

In respect to long-term effects, no significant main effect was registered between dancers and nondancers. However, a profound understanding of the symbols in the Labanotation revealed no mental rotation costs, thus suggesting that the symbols were transformed in an abstract form of body representation.

Table 8.

Short- and Long-Term Effects of Representations in Different Sensory Systems.

Sensory System	Response Mode	Short-Term Effects	Long-Term Effects
Vision (1)	Reaction Time Response Accuracy	Visual Stimuli Type (Object vs. Body vs. Symbol) Stimuli Orientation (Front vs. Back)	Imagery Training (Symbol Knowledge)
Somatosensory (2)	Response Bias (Motor or Visual)	Type of Response (Motor vs. Visual) Amount of Stimulation (Tactile Stimulus vs. Double Tactile Stimuli) Type of Sensory Stimuli (Visual vs. Proprioception)	Proprioceptive Training (Dancers vs. Nondancers)
Motor (3)	Movement Parameters (Strength, Reaction Time, Movement Range)	Type of Stimuli/Task (Anticipation vs. Eyes Closed)	Motor and Motor Imagery Training

2) Somatosensation

In the chapter 3 on somatosensory signals, two types of adaptive body representations were found with respect to the sensory modes proprioception and tactile sensation. In Experiment 4, proprioceptive body representation was based either on visual or proprioceptive information or both. The data showed that locations in the egocentric space were biased by two reference points, one at each shoulder, when proprioceptive information was provided. However, with visual information alone, a superordinate body representation with one reference point at the centre of the trunk was found in the case of existing motor expertise. Therefore, proprioceptive representation was adaptable with respect to the mode of sensory information received in short-term (vision or proprioceptive information) as well as with respect to motor expertise in long-term (dancers vs. nondancers). The data in Experiment 5 showed that the perceived body surface can swap immediately. Tactile stimuli applied on the forearm evoked a body representation with the trunk as the attractor. Tactile stimuli were perceived closer to the trunk than where the stimulation was applied. However, when tactile information was additionally received at the tip of the fingers of the stimulated hand, the point of attraction changed from the body centre to the periphery. The tactile stimuli were felt more peripherally than where they were actually applied. Thus, short-term adaptability of the body representation in response to tactile information at different locations on the body surface can be assumed.

Long-term effects were evident by significant differences between dancers and nondancers with dancers being generally more accurate than nondancers in matching the arm position in egocentric space based on proprioception. Also, the data suggests that dancers generate a mental proprioceptive image of their body limbs in space.

3) Motor

Finally, chapter 4 showed strong evidence for short- and long-term adaptability in a motor learning task. A movement without an established motor command could be executed quicker by imagery training than execution training or no training (i.e., training of a control movement). Additionally, participants were showing a bigger movement range when the point of maximum abduction was visually anticipated.

Modular Representations versus Multisensory Integration

Multisensory information is integrated to provide a coherent representation of the body in a multidimensional environment. Therefore, a model of cognitive processes should take consideration of these multisensory signals. However, a modular view of cognition still dominates many theoretical assumptions in cognitive neuroscience. Fodor (1983) was most prominent in the modular perspective. In the modular theory of mind, the mind is regarded as compositions of independent, closed, domain-specific processing modules – manifested in cortical areas that are receptive for a specific associated sensory system. For example, visual information is processed in visual areas in the occipital cortex, while sensorimotor and motor information are processed in the parietal sensorimotor and motor cortex, respectively. However, the body is phenomenologically experienced as a whole. The data discussed in this thesis also account for adaptation processes as part of multisensory integration. The experimental results suggest that representations based on various sensory systems are similar with respect to their short- and long-term adaptabilities. A model of the cognitive system that connects and integrates different sensory

perceptions to adapt mental representations and images accordingly, seems therefore more likely than a modular system. Other behavioural effects were reported that further account for multisensory integration. For instance, the McGurk effect (McGurk & MacDonald, 1976) in speech perception shows that conflicting sensations from vision and audition are automatically interpreted by the brain as an intermediate solution. Furthermore, a model of a representation based on multisensory integration or multisensory fusion is in line with recent studies on cortical processing (Macaluso, 2006). Cortical areas that were previously reported to be sensory specific show clear cross-over effects from different sensory systems. Therefore, the existence of disparate body representations - each linked to a singular sensory system or each based in modality representations in multimodal brain areas - has to be questioned.

From an economical perspective, it seems unwise to propose a body representation for each sensory system or modality. The brain needs to be organised in a way to process multisensory information. According to the theory of modality-specific body representations, sensory information would need to be transformed into different representations in order to create a coherent sense of the self. I would propose a model with a single representation that is highly adaptable. The data from this thesis supports such a representational platform. Short- and long-term adaptability in response to the characteristics of the representation has been found. For example, short-term adaptabilities observed were the orientation of body stimuli in Experiment 2 or the symbol level in Experiment 3. Long-term adaptabilities measured were for example the general level, of expertise in Experiment 5 or the process level in Experiment 6, where performance effects of imagery training are compared to execution training.

However, none of the experiments cover all the possible dimensions of body or movement representations that can be sensitive to adaptability mechanisms. The dimensions of cognitive tasks can be described by three primary activities: firstly by a perceptual input, secondly by mental operations, and thirdly by the output and response. In comparison, physical activities can be structured in strength, endurance, and movement qualities. Driskell et al. (1994) mentioned these classifications in reference to studies in more applied fields. Nevertheless, I used these dimensions for a deeper understanding of the results of the body and movement representations adaptability.

In some of the experiments conducted on body representation, the visual inputs of the stimuli as well as the output and response modes were modified. The visual input stimuli were modified in the experiments on visual and proprioceptive sensory perception while the response was varied in the experiment on tactile perception. The movement representation was investigated by measurements in all three physical activity dimensions, strength, endurance, and movement quality as force, training endurance, and movement range. Furthermore, the visual input was modified when testing the movement range. A complete model of the body representations adaptability, however, should be based on a balanced selection of input and output modifications in all sensory systems. Only the investigation covering movement representation used a broader range of dimensions (e.g., movement reaction time, abduction amplitude, etc). Nevertheless, the physical dimensions are investigated in one single novel movement. The lack of a broader balanced selection of all dimensions and different forms of movements would not influence the impact of the singular investigations. However, it is worthwhile to consider these in order to achieve an

appropriate image of the human representations adaptability as well as for further investigations on this matter.

Functionality of Representations

Based on the reported findings, I suggest that the optimal use of the term ‘representation’ is to describe a network within the brain that provides a constantly adapting platform. The adaptations are changes with respect to the state of the brain, which is actually both dependent of the relation between the body and its environment as well as responsible for the bodily behaviour in the environment. Many researchers prescribe to the idea that humans have several forms of images, such as visual, spatial, and motor images as well as several body representations, such as body image or body schema. Further, several motor representations are assumed for each set of motor programs, or at least for each chunk of our skilled movements. Unfortunately, the various terms are often confused. This is particularly the case for the terms associated with body representations. Instead of relating different forms of representation to different functions, one can increase the understanding of the human body and brain by investigating the processing rules or characteristics that underlie most of these body and movement representations.

Adaptation

It often seems that ‘adaptation’ is used as a catch-all term. Generally, it stands for a persistent change in a system in response to environmental stimulus or input.

This means, in this thesis, the term ‘system’ refers to the representational processes in the human brain and their adaptations to the changing environment, which are actually the sensory information from the external world as well as the information from internal mental states. It is important to note that looking at mental representations in the form of a system has several implications. First, it helps to draw a line between modifications in the mind from changes in the body (neuromuscular system) and the brain’s structure (cortical maps). In the former, the term ‘training’ is used to describe a form of adaptation processes. In the latter, however, the term ‘plasticity’ is used in several studies to indicate how the organisation of cortical maps changes over time (for a review see Pascual-Leone, Amedi, Fregni, & Merabet, 2005). Second, it helps looking at the functional role of representations in respect to the mind. How can representation be of importance to the mind as a system?

Another form of adaptation is within sensory systems on the level of sensory receptors. Receptors that receive the same information over a certain amount of time adapt and change their behaviour. For instance, receptors in the retina adapt to darkness. In the tactile system fibres are categorised as fast adapting and slowly adapting fibres with respect to their responses to sustained indentation of the skin. Other adaptation processes can be found in the olfactory, gustatory, and thermal system. To summarise, adaptation on the receptor level describes how the neural system deals with constant information. Therefore, the interplay between change and constancy in adaptation is an important feature of the body. It is notable that even though considerable plasticity in the neuronal representation of the body surface in the somatosensory cortex was shown, representations are also stable to a certain extent. For example, during the

course of a recording session the receptive fields of particular neurons may remain fixed (Kass, Nelson, Sur, & Merzenich, 1981). Lackner (1988) suggested that this stable organisation, however, may be a result of balancing dynamic influences. When the balance is unsettled by inactivating part of the peripheral sensory input, the organisations of the cortical maps are immediately altered and continue to change over time.

Functional Model for Representation and Imagery

Various forms of representations in respect of content and their sensory basis have been discussed in recent literature. Within this thesis, adaptation effects of representations in each sensory system were found. However, instead of looking at the content of various representations, the focus herein is on the functional properties. Central are questions like "*how* do representations and imagery processes function?" and "*why* are representations and imagery built?". Pani (1996) wrote an important review on such a functionalist perspective on mental images. Descriptive for this perspective is that the mental image is not viewed as "… a static hard existence, but a fluid fleeting thing, moulded by every exigency of the momentary task" (Pani, p. 37; quoted from Downey, 1929). Images and representations are not isolated mental objects with fixed properties. "An image provides representation in the adaptive regulation of activity, and this more or less local role will influence the structure of the image" (Pani, p. 294).

The title "Body Representation and Motor Imagery: Effects of Adaptability" can be read twofold. First, several short- and long-term adaptabilities in body and movement representations based on various sensory systems as well as affected by motor imagery were found. Therefore, a similarity between all forms of

representations is their adaptability to various stimuli and responses. Second, the adaptability may be the grounding of representation and mental images. Representations enable a constant interaction between the adaptive cognitive system and the changing environment. Therefore, I hypothesise that we have a single form of representation, which is able to adapt to various sensory input and output forms and of which parts are conscious. The latter form is described as images. Whether parts of the representation become conscious or not may be dependent on the novelty and difficulty of the task. *Adaptation is the basic characteristic of representation and at the same time the only reason for mental representation. Without the necessity of adaptation processes no representation would be necessary.* Adaptation is thus considered as the cause and representation as the effect.

Connectivity of Body and Movement Representations

It has been proposed in the introduction to look at both body and movement representations' adaptability as we not only own and perceive our bodies; we are also agents of most of our own bodily movements. We are constantly moving our body, so movements are a particular feature of humans and animals. Also, both the spatial perception of body limbs (position sense) and the perception of passive movements (movement sense) play a part in sensory perception as shown by sensory disturbances in cerebral lesions. As stated in the early work of Head and Holmes (1911) the authors describe why cortical lesions most frequently disturb the recognition of posture and of passive movements:

> Inability to recognize the position of the affected part in space is the most frequent sensory defect produced by lesions of the cerebral cortex. In some cases, this and the allied faculty of recognizing passive movement may be the only discoverable abnormalities. Whenever sensation is disturbed at all, these two forms of special recognition will be certainly affected. (p. 157).

Furthermore, in all the cases stated in Head's paper, the disturbance of recognising posture and passive movements was shown to be greater towards the peripheral parts of the affected limb. Certainly, the studies outlined here indicate indeed that body and movement representations share common features. In particular, they both showed evidence of being highly adaptable.

Outlook

From behaviourism to cognitive science to cognitive neuroscience – what comes next? Within this thesis, representations were considered as based on the necessity of adaptability processes. This has one relevant implication to consider; the individuality of mind. The bigger the role of adaptation processes is acknowledged, the bigger the individual differences in the cognitive processes have to be assumed.

It was in the era of cognitive science when scientists looked into the black box and determined mental representations and images. Later, with the use of new techniques in cognitive neuroscience, a few more cognitive processes could be localised in the human brain in a noninvasive way. Radical behaviourists thought that humans and animals show the same behaviour. Learning and adaptation mechanisms were understood to be only dependent on stimulus and response while cognitive matters were completely ignored. Somewhat similarly,

today individual differences are only partly investigated. In most experimental studies, participants are thought to behave relatively similar. However, despite investigations in neuropsychology focusing on particular cases, the subject is still viewed from a collective perspective. Experimental studies test significant differences between conditions or between different participant groups. However, with the knowledge of the present high adaptability factor, it seems that individual differences and individual neuronal consolidations cannot be overlooked anymore. The emphasis on individuality in representational concepts as it is expressed in here is, thus, not unique.

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Successful Research Grants

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